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SEVEN YEAR HERITABILITY ESTIMATES
FOR PONDEROSA PINE IN THE NORTHERN ROCKY MOUNTAINS

By

Virginia K. Graham

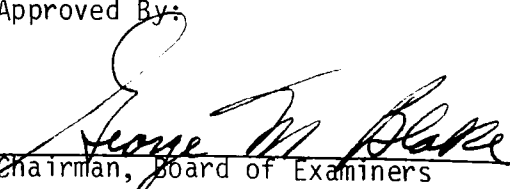
B.S., University of Montana, 1977

Presented in partial fulfillment of the requirements for the degree of
Master of Science in Forestry

UNIVERSITY OF MONTANA

1982

Approved By:


Chairman, Board of Examiners


Dean, Graduate School


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ABSTRACT

Graham, Virginia K., M.S., June 1982

Forestry

Seven Year Heritability Estimates for Ponderosa Pine in the Northern Rocky Mountains (117 pp.)

Director: George M. Blake



Genetic variation in seven year total height of ponderosa pine (*Pinus ponderosa* Laws.) was estimated by the common environment garden method. Seven test plantations provided different environmental conditions throughout the Northern Rocky Mountains. Each plantation contains randomized block plantings of 434 open-pollinated families representing 93 stands selected within the Inland Empire. A two-way analysis of variance, with proportional subclasses, for each plantation and subsequent F-values showed that families, blocks and the block X family interaction have significant ($\alpha = 0.01$) effects on seven year total height of the progeny. Narrow-sense heritability estimates at each plantation indicated substantial genetic variation and that this species will respond favorably to selection. Multiple comparison procedures applied to family mean total height at seven years produced different family rankings and different contrasts between plantations. Simple linear regression analyses and scattergrams plotted by plantation exhibited nonsignificant associations between family total height and environmental factors at the seed source origin.

ACKNOWLEDGEMENTS

My sincerest gratitude and appreciation are extended to all those who assisted in this project. It is a distinct pleasure to acknowledge my committee chairman and advisor, Dr. George M. Blake. He had faith and confidence in my abilities, and provided continuous encouragement and support in times of frustration. He also secured financial assistance for me through the McIntire-Stennis Fund.

A very special thanks to Dr. Hans R. Zuuring for his technical advice and for sharing his expertise during the data analysis portion of this study. His constructive criticisms and candor throughout the development of my thesis were invaluable.

Appreciation is also expressed to the members of the Inland Empire Tree Improvement Cooperative for their help with the field measurements, and also to those individuals who demonstrated special interest, including Dr. Sherman J. Preece, Jr. and Dr. George L. Card who generously gave their time to serve on my committee.

For their long, tedious hours spent reviewing, typing, editing and proofing the various phases of my work, grateful thanks to Pat Graham, Judy Revere, Marica Koverman and Ron Knorr. Space is not sufficient here to mention all the other friends who have helped and encouraged me to complete my graduate program. To individually acknowledge their contributions would be impossible, but their inspiration and support are deeply appreciated.

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INTRODUCTION

Background

The increasing demand for wood on a shrinking forest land base, coupled with predicted future demands for wood production, emphasize the importance of increasing forest yield through silvicultural and genetic improvement programs. Silvicultural systems that rely on natural regeneration often result in either inadequate regeneration or regeneration with changes in the forest composition. Silvicultural practices now lean toward artificial regeneration with cultural and genetic improvements. In its broadest sense, genetic improvement constitutes another silvicultural alternative used to obtain greater production from forest lands. Considered alone, genetics verges on the academic, but used along with proper site preparation, competition control, and other silvicultural treatments, it provides the key to maximum timber production on forest lands. Genetic improvement alone will be ineffective, while standard silvicultural treatments without the use of good genetic stock can only prove partially successful.

Even though often considered a silvicultural tool, genetic manipulation of forest trees possesses certain unique characteristics: 1) a genetic change is "permanent", unlike the temporary influences of fertilization, competition control or site preparation; 2) most insect or disease pests can be efficiently controlled only through the development of tolerant strains of trees; 3) new strains of forest trees can

be developed for better adaptation to marginal or submarginal sites and enable the maintenance or expansion of the productive forest land area; 4) man can refine and use different strains for his benefit while preserving the bulk of the gene base for new needs that might develop in the future; and 5) through selective mating and hybridization, it is possible to create trees with characteristics not available in nature.

Presently, there is no way to ascertain how well a seed from one area will perform if planted in an area of different climatic and environmental conditions. The expected success of seed germination, survival, growth and volume production must be known before planting to avoid costly mistakes.

Current economic analyses of tree improvement, as an investment opportunity in the northern Rocky Mountains, are estimated to yield a 6% rate of return (Keegan 1976). Ponderosa pine (*Pinus ponderosa* Laws.) is the most economically important pine species in the western United States. In the Inland Empire, its stumpage value is exceeded only by western white pine (*Pinus monticola* Dougl.) and western red cedar (*Thuja plicata* Donn.) (Swift 1976). Ponderosa pine has the largest native geographic range of all pines in North America. This wide distribution extends from the Fraser River Valley in British Columbia, south to Mexico, and from the Pacific Coast inland to Nebraska (Critchfield and Little 1966). (Figure 1.)

This economically important species has been the subject of several intensive genetic research programs. However, little knowledge exists about the potential of ponderosa pine to respond to genetic

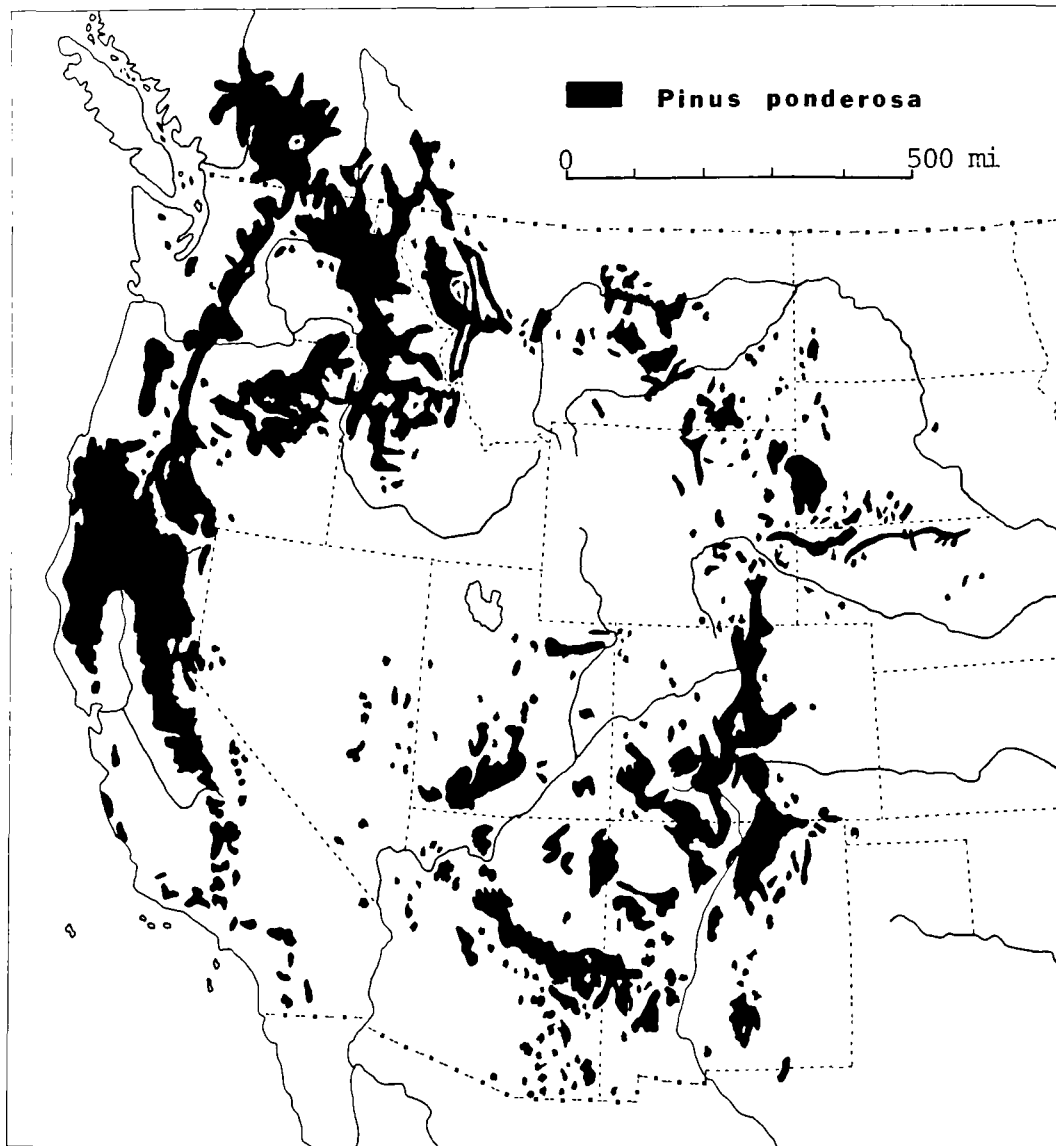


Figure 1. Geographic Distribution of Ponderosa Pine

selection for growth traits. Previous studies have demonstrated that genetic variation in relation to growth characteristics does exist in ponderosa pine (Weidman 1939, Callaham and Liddicoet 1961, Squillace and Silen 1962, Wells 1964, and others).

These studies have either been of broad geographic variation (Weidman 1939, Wells 1964), or very narrow in scope (Callaham and Liddicoet 1961, Wang 1974). In addition, very little of this work directly involved the production of genetically improved stock for use in reforestation programs. Up to 1970, only 20 acres of ponderosa pine seed orchards existed in the United States (USDA 1973). To date, research has provided initial genetic variation information about ponderosa pine from nursery performance. Heritability is an estimate of the extent to which variation in characteristics (phenotypic variation) may be conditioned by variations in the genotype of the trees (genetic variation).

Geographic variation studies are essential for tree improvement programs, because the establishment and subsequent fitness of seed sources depends on an accurate definition of suitable environments (Madsen 1975). Early provenance research has established that nearly all forest tree species exhibit strong adaptive variation. New approaches to studying forest tree species combine morphological, biochemical, physiological, ecological, and genetic investigations with modern statistical methods.

Long Range Plans

This study represents a small part within a much larger project initiated by the Inland Empire Tree Improvement Cooperative (Appendix A). The working hypothesis of the overall project states that genetic variation of ponderosa pine in the northern Rocky Mountains relates directly to the complex gradients associated with mountain topography. If so, genetic variation attributable to parent tree location would best be described by a topocline. The hypothesis originates from the concept that for any area delimited in space and time, the range of environments can be represented by an average effect and deviations from that average. For plants within such an area, an analogous average genetic effect and deviations exist because adapted plant types occur in proportion to the environment (Levins 1969). If there is a gradient change in the environment at several adjacent locations, there should also be a gradient change in genotypes forming a cline (Levins 1963). Further, genetic variation among plants within locations along the same gradient can be expected to be proportional to the number of plants sampled (Donovan *et al.* 1976). The project will provide quantitative information about genetic variation as well as qualitative information about environmental variation and the interaction between the two. The former yields valuable insights to the adaptive strategy of ponderosa pine. The latter provides a quantitative assessment of the degree of differentiation along environmental gradients.

Objectives

This study was an examination of genetic variation in seven year total height growth for 434 selected individual families of ponderosa pine. The specific objectives were: 1) to describe patterns of genetic variation with respect to seven year total height; 2) to estimate the proportion of seedlings that will be nonadapted in transfers from one location to another for the identification of seed planting zones; 3) to estimate individual family heritabilities as related to height growth; and 4) to make recommendations for future ponderosa pine genetic improvement work.

Procedures

The genetic variation in ponderosa pine was estimated by the common environment method. The method involves progeny from various parent trees grown on common test sites. This method can nearly equalize the environmental component factor contributing to phenotypic variance for each individual on the test site. Phenotypic (or observed) variance (σ_p^2) may be grouped into two categories: genetic variance (σ_g^2) and environmental variance (σ_e^2). By definition: $\sigma_p^2 = \sigma_g^2 + \sigma_e^2$.

Thus, the phenotypic or measurable variation at the test sites were used as indicators of genetic variation between individuals. Variation in height and diameter growth characteristics between different families at different, but known, environmental situations provided the basis for determining the heritability of these characteristics.

Data used in the analyses of genetic variation came from seven year total height measurements at seven test plantations. Each plantation has different environmental conditions. An analysis of variance was used to determine the relative amounts of genetic variation within and between families, and within and between stands. From the analysis of variance, narrow-sense family heritability estimates were calculated for each plantation.

Results from this study provide a vital step in the development of seed transfer rules and breeding zones. A resultant seed zone planting guide will allow the identification of the best seed source collection areas for use in artificial reforestation of ponderosa pine.

LITERATURE REVIEW

Genetic Variation in Forest Species

Several researchers (Squillace and Silen 1962, Wells 1964, Allard 1965, Squillace 1966, Herman and Lavender 1968, Rehfeldt and Lester 1969, Roche 1969, Kung and Wright 1972, Madsen 1975, Brown 1978 and others) have reviewed genetic variation of forest species in depth. Therefore, the references selected for inclusion here meet one or both of the following criteria: 1) recent or pertinent review articles, symposia, etc. which afford effective entry to the literature; 2) illustrative examples of particular types of work.

The term "genecology" was first used by Turesson (1923) to study the intraspecific genetic variation of plants in relation to their environments. A genecologist primarily seeks to determine habitat correlated, genetically based variation within a species. Madsen (1975) has an indepth review of genecology concepts, and the evolutionary and physiological aspects of genecological differentiation. The central thrust of genecology has been to partition the genetic variance of populations in such a way that the characteristics of interest can be measured and evaluated.

Ecosystems follow the diversity-stability rule. As diversity increases, stability increases (Odum 1969). This rule applies not only to ecological food chains and species diversity but also to diversity as measured by the heterozygosity within populations (Tigerstedt 1974).

Adaptive changes in a population generally result from mutations, migration, genetic drift and selection pressures. A compromise will always exist between fitness for the present environment and the flexibility for adaptation (Mather 1943, Darlington 1958, Metter and Gregg 1969). Survival and reproduction of individuals in their immediate environment requires fitness. Production of progeny preadapted to environmental change necessitates flexibility. Therefore, if species cannot adapt to change and lack genetic variability they may face extinction (Thoday 1953). However, species with high genetic variability may be unable to produce preadapted progeny, and therefore they cannot compete with better adapted species (Mather 1943). This fitness-flexibility compromise occurs in all species. The advantages of recombination are balanced with the disadvantages of segregation, i.e., gene combinations with high fitness can be formed in recombination, but they also may be dissolved in segregation (Madsen 1975).

In populations adapted to variable nonhomogeneous environments, more genetic variability can be expected than in highly specialized populations in homogeneous environments (Thoday 1953, Bradshaw 1965). Therefore, genetic variation patterns are determined by properties of the genetic system and the type of environmental variation encountered. Different variation patterns along the same geographic gradients within the same species, but for different characteristics, are also common (Ehrlich 1969). Various characteristics encounter specific components of the environment and react to them accordingly (Stern and Roche 1974). Thoday (1953) has considered alternative adaptive strategies as

a conflict between adaptive differentiation (specialization-fitness) and phenotypic plasticity (flexibility). Specialized populations have become genetically attuned to different environments. Under phenotypic plasticity, the development of variable phenotypes allows adaptation to heterogeneous environments. Genetic variability is not necessarily expressed phenotypically and not necessarily exposed to selection, therefore is conserved (Rehfeldt 1979a).

Levels of Genetic Variation

Genetic variation in natural populations of forest trees exists on several different levels. The first involves the level of geographic variation. This level is frequently referred to in the literature as provenance. In the western United States, variation between interior and coastal Douglas fir, Black Hills and Sierra ponderosa pine, and Southern California and Sierra white fir exemplifies this level. Another example shows the difference between coastal plain and piedmont loblolly pine. By contrast, in New England and the Lake States, red pine serves as a good example of a relatively widespread species which does not contain a significant amount of genetically controlled geographic variation. This term implies evolutionary adaptation to the environment which may occupy large areas, or change slowly over large areas. It also implies a general level of adaptation throughout large subregions of the species range and differences in such adaptation between those subregions. This concept holds equally valid relative to subspecies, races, or clines within species, as long as the distance and selection pressures remain great enough to maintain general subrange adaptability against the long-term forces of genetic change.

The second level of genetic variability occurs from stand-to-stand within a geographic region. This may be either long-term, relatively stable local adaptation, or more transient local genetic variability. The long-term variability perpetuates when stands occur in peculiar environmental conditions or in well enforced genetic isolation from any other nearby stands. Lodgepole pine occurring on the Mendocino white plains in California may provide an example of unusual stands on unusual soils. More transient stand-to-stand variability may occur through genetic sampling errors when a population passes through a bottleneck. The history of loblolly pine invasion of old fields from the few parent trees bordering the field may lead to such variation (Stonecypher, Zobel and Blair 1973). It may also occur when short term, but intense, selective forces have been at work in some stands in the region and not in others. High-grading by man provides one of the most powerful of these selective forces. Damman (1964) stated, for example, in some stands in the northern hardwoods, high-grading has occurred while other stands have had the effects of excellent silvicultural practices.

Variation between individual trees within a stand demonstrates another level of variability. Although the amount of variability is a long-term characteristic of a stand, specific genotypes normally last for only a single generation. Much theory and an increasing amount of experimental evidence supports the general principle that forest tree species contain a high degree of tree-to-tree genetic variability within local populations. Outcrossing mechanisms, normally operating within

forest tree populations, maintain and reconstitute this variability from generation to generation. Thus, a great diversity of genotypes within a single stand can be expected, both relative to characteristics biologically important to the trees, and economically important to man.

Clinal variation can usually be recognized on the basis of morphology, but appears to be almost always accompanied by a gradation in the physiological features. Clinal variation provides a genetic condition for high value in terms of tree improvement. Some of the most important timber species display this type of variation throughout their range, and therefore a knowledge of such patterns is of great significance when searching for the best provenance for any particular silvicultural use.

Patterns of Genetic Variation

Ideally, to interpret the total variation patterns of a species, a combination of range-wide, regional, and local studies should be utilized. Provenance studies can delineate certain widespread, often climatically adaptive traits; but these studies often imply discontinuities in certain traits because of the broadly spaced sampling schemes. The studies which sample intensively on the local or even regional level are more sensitive in sorting out genetic variation patterns (Madsen and Blake 1977).

Two main factors complicate the interpretation of genetic variation patterns in a species. First, very few species have been adequately sampled throughout their entire range. Until now, the complexities of the variation patterns directly reflect the scale on which the

original studies were conceived. Numerous studies of forest tree species reveal that significant, environmentally correlated, genetic variation can exist between populations within a relatively small geographic area. Sakai and Park (1971) found significant genetic differentiation in peroxidase isozymes in their studies of three adjacent populations of *Cryptomeria japonica* D. Don. In high elevation *Eucalyptus urnigera* Hook., Barber (1959) found the leaves to be 100% glaucous, whereas only 550 meters lower in elevation this characteristic was not evident. Significant differences in both isozyme frequencies and morphological characteristics were observed by Feret (1974) in his studies of *Pinus pungens* Lamb. stands that were 18-42 km apart. He suggests that since the stands had similar environmental conditions, genetic drift along with some unidentified environmental factors may have contributed to the varying gene frequencies.

Within narrow geographic areas, studies of genetic variation should be contrasted with range-wide studies of forest species. These types of studies usually consist of widely spaced population samples throughout a large range of the species. A few examples of this type of study include Barber's (1964) study of slash pine (*Pinus elliottii* Engelm.), Hamrick and Libby's (1972) study of white fir (*Abies concolor* (Gord. and Glen.) Lindl.), Critchfield's (1957) study of lodgepole pine (*Pinus contorta* Dougl.), Langlet's (1934, 1936) study of scotch pine (*Pinus sylvestris* L.), and Wells' (1964a, 1964b) study of ponderosa pine (*Pinus ponderosa* Laws.).

Second, the identification of environmental variation patterns are influenced by the researcher's interpretation. For example, what may be ecotypic variation to one person may merely represent a steepening of the environmental gradient, in a clinal pattern, to another person (Madsen 1975).

These existing problems in determining variation patterns show that higher taxonomic subgroupings are not only valueless (Langlet 1971) but harmful (Huxley 1939). They imply homogeneity (which is non-existent) within conventional units which are really abstractions. Such broad general subgroupings of species has led to serious, costly mistakes in artificial regeneration with the planting of stock not adapted to the environment (Langlet 1971).

Isozyme Studies

Electrophoretic analysis of genetic diversity in populations can be used to complement techniques of quantitative genetics for assessing genetic variability in the species of interest. Most populations seem to be polymorphic for electrophoretic patterns in at least some enzyme systems.

Robertson and Reeve (1952) discovered that the environmental variance of a particular genotype appears to be intimately related to the degree of heterozygosity. The more heterozygous individuals carry a greater diversity of alleles which will likely endow them with a greater biochemical versatility in development. This leads to heterosis because of more efficient use of materials available in the environment and a reduced sensitivity to environmental variations.

More ways will be available to overcome obstacles, caused by such variations, that interfere with normal development .

Sakai, Miyazaki and Matsuura (1971) have worked with peroxidase isoenzymes of leaf characters in needles of *Thujopsis dolabrata* Sieb and Zucco. They have demonstrated that two natural populations separated by 10 km wide straits are significantly different with regard to the occurrence of peroxidase isoenzymes. The same difference also occurred in leaf characters. They continued investigations and found indications that the trees in natural forests are more homogeneous than expected from random mating (Sakai, Miyazaki and Matsuura 1972).

Allelic variations in white spruce (*Picea glauca* (Moench) Voss.) were studied by Feret (1971). He stated that most isozymes are developmentally stable, so it is theoretically possible to achieve a very close approximation of allelic variations in a tree species. Isozyme variations can be directly related to a heterozygous or homozygous state at a single locus. The author's results indicate that isozymes are under genetic control, and the number of isozyme combinations are greatest in open-pollinated families and smallest in self-pollinated families.

Rasmuson and Rudin (1971) found considerable individual variation which presumably is genetically determined. Their study of esterase enzyme systems in scotch pine (*Pinus sylvestris* L.) showed considerable variation between individual trees. The authors state that analyses must use enzyme systems with individual variation and environmental stability, and that the next step must be the study of offspring with known descent. Then it may be possible to find an association between

the marker loci and economically important characteristics, i.e., hardiness and growth. They also propose that if a number of genetic polymorphic enzyme systems become known, they can give information about the origin and degree of inbreeding for special trees and about genetic differentiation between and within populations of forest trees.

The results of Burdon and Zabkiewicz (1973) indicate that monoterpene analyses could be a promising technique for establishing the genetic identity of individuals. Other results confirm that genetically identical and nonidentical seedling twins can occur in Monterey pine (*Pinus radiata* D. Don), and therefore twins originate from both cleavage and archegonial polyembryony. The authors conclude that since monoterpenes abound in all conifers and are analyzed easily, the applications of the technique could be widespread.

Starch gel electrophoresis was used by Fowler and Morris (1977) to survey for genetically determined enzyme mobility differences among 297 megagametophytes of red pine (*Pinus resinosa* Ait.) from five widely scattered geographic areas. Consistent and reproducible enzyme banding patterns were observed in five of the seven isozyme systems assayed. No variation in band mobility was observed in any of the systems. The results correspond with the low degree of genetic variation observed in red pine for higher levels of genetic organization. However, the results conflict with those reported from surveys of allozyme variation in other coniferous species. The authors conclude that red pine is genetically depauperate. All 297 female gametophytes produced identical enzyme banding patterns. Evidence indicates unusually low levels

of genetic variability within and between populations (Fowler 1965). The conclusion, based on current data, states that the average heterozygosity per locus in red pine equals zero (Fowler and Morris 1977).

Guries and Ledig (1978) studied the inheritance of eight polymorphic isoenzyme systems encoded by 14 loci of pitch pine (*Pinus rigida* Mill.). Two enzymes demonstrated variants segregating in a pattern suggestive of single locus control. Five enzymes showed two zones of segregation, suggesting dual loci control. Finally, one enzyme exhibited three zones of activity. No evidence of genetic linkage between pairs of heterozygous loci in the same or another tree could be detected. These results closely resemble those of Simonsen and Wellendorf (1975) who studied the zymogram patterns of these isozymes in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) endosperm.

O'Malley, Allendorf, and Blake (1979) studied the segregation of isozyme variation in individual ponderosa pine (*Pinus ponderosa* Laws.) megagametophytes. They confirm the 1:1 expected Mendelian segregation in the gametes from heterozygotes. They observed a high amount of genetic heterozygosity in ponderosa pine as compared with other plant species. The authors estimated that approximately 12% of the genetic variation detected can be associated with genetic differences between stands. They concluded that ponderosa pine in the northern Rocky Mountains is not strongly geographically differentiated at the loci examined. The stands chosen include an ecologically, geographically and genetically diverse sample and represents the range of variation found in the Madsen and Blake (1977) study.

Survival Studies

Gashwiler (1967) studied naturally disseminated seed survival in a clear cut area of the H. J. Andrews Experimental Forest in the western Oregon Cascade Range. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western red cedar (*Thuja plicata* Donn.) showed different survival rates from seed fall until the end of germination. The reasons for the differences varied depending on the species and included birds, rodents, drought and temperature. Survival during the same period for Douglas fir, western hemlock and western red cedar were respectively 12%, 31% and 65%.

Morgenstern (1969a) found that the population variation was largest for the phenological and morphological characteristics of black spruce (*Picea mariana* Mill.). For six characteristics related to germination and drought resistance, the family variance (expressed as a percent of the total) was largest. The variance of subpopulations was very small and never exceeded the family or population variance. On the basis of criteria adapted for this study, genetic variation in black spruce is essentially clinal (Morgenstern 1969b).

In black walnut (*Juglans nigra* L.) during the first ten years, Bey (1979) found survival unrelated to the seed origin except in the Minnesota planting. In Minnesota, only 25% of the trees originating 300-600 miles south of the planting site survived, versus 70% for more northern trees. Diameter growth differences were apparent in all plantations, and height growth differences related to seed origin were

observed in all plantations except Missouri and Kansas. At these locations, the cold, dry winter of 1976-1977 was hard on the trees. Although only a small percentage died, crown dieback was severe and definitely related to the southern origin of the seed. Bey (1979) concluded that trees of southern origin tend to be faster growing and less cold hardy than those of northern origin.

Freezing tests on Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco.) indicate that hardiness develops at a rate associated with minimum temperature (Rehfeldt 1977). Variation in the hardiness of populations relates to geographic and ecologic factors of the seed source during the early stages of cold acclimation. Multiple regression equations account for 38% of the variance among populations and show that populations of greatest hardiness in early autumn originated from relatively high latitudes, high elevations and cold environments. However, variation among populations in hardiness during late stages of cold acclimation could not be related to factors of the seed source.

At Fort Valley, Arizona, Larson (1966) found poor survival of ponderosa pine (*Pinus ponderosa* Laws.). Eleven of nineteen sources survived and no source exceeded 40% survival. The pattern clearly reveals that sources from the eastern and southeastern part of the range survived, while northern and western sources failed. Insects and unfavorable weather accounted for most of the mortality in early years. Seedlings from the north and northwest were unable to withstand the frost and drought periods of the southwest. Sources closest to Fort Valley grew best, and the Black Hills sources grew well in some

instances. Black Hills and central Rocky Mountain trees typically consisted of 2-needle fascicles while trees from the southern Rocky Mountains grew longer needles, usually in fascicles of three.

Tauer, Mohn and Cromwell (1974) documented evidence of differential survival between regional groups of ponderosa pine grown at four locations in Minnesota. On the basis of early survival, the authors suggested that seed from southern and far western collections be avoided in Minnesota. At all plantations, differences among mean heights of regional groups showed statistical significance ($\alpha = 0.05$). Using Duncan's multiple range test, the authors compared groups within plantations. Generally, seed originating north of the 43rd parallel performed better than other seed sources. The Big Horn seed source, which came from a relatively high altitude, was an exception. Southern and far western sources performed below average in height growth and had low survival in all plantations.

Analysis of ponderosa pine survival data by Deneke and Read (1975) indicate significant differences among both provenances and blocks. Generally, the lowest survival occurred in sources from west of the Continental Divide and from the southern Rocky Mountains. Survival of progeny derived from natural stands in southeastern Montana, eastern Wyoming, North and South Dakota, eastern Colorado and Nebraska were generally good. Sources that survived the best were from diverse locations throughout the northeast part of the range. Thus, no well established patterns could relate survival to latitude or elevation of the parent stands. Analyses of height growth data showed significant

source effects, and results from regression analyses indicated that elevation significantly (inversely) affected height growth.

A ponderosa pine provenance test plantation in Central Oklahoma showed 62% overall survival with most of the mortality occurring in the first summer after planting (Tauer and Gardner 1978). Analysis of variance on the nine year survival data indicated significant differences ($\alpha = 0.05$) among seed sources and geographic ecotypes. Duncan's multiple range test indicated differences among sources. This test showed the best eight sources significantly ($\alpha = 0.05$) different from the remaining sources, but no differences existed between those eight. Significant differences ($\alpha = 0.05$) also appeared in nine year growth rates among provenances and among ecotypes. As with survival, the fastest growing sources originated from east of the Continental Divide in Montana, Wyoming, and Nebraska. On the basis of both survival and growth rate, the best seed collection areas for planting in Oklahoma are located in central Montana, the northern high plains ecotypes and the northeastern sources of the low elevation east plains ecotype. These sources also show promising performance in Minnesota (Tauer *et al.* 1974), the Black Hills (Van Deusen 1974), and Kansas (Deneke and Read 1975).

Growth Studies

Baldwin (1956) measured terminal growth during two seasons on a nine and ten year old European larch (*Larix decidua* Mill.) provenance plantation in New Hampshire. He observed: 1) that all sources completed 50% of their growth at approximately the same date; 2) the

beginning date of growth varied as greatly within as between provenances; and 3) air temperature was associated with bud bursting. No correlation was found between either altitude or latitude of seed source and the amount of current height growth or the mid points of the growth curves.

Western white pine (*Pinus monticola* Dougl.) data on early growth rate was assembled by Squillace and Bingham (1958). They studied progenies of trees from different selection areas and found the existence of inherent growth rate differences between some of the areas. The use of pollen parents from "better sites" usually resulted in faster growing progenies than pollen parents from "poorer sites". Progenies of selections on "better sites" grew an average of 10% faster than those of selections on "poorer sites". Both differences in average growth rate between individual areas and between site groups were highly significant ($\alpha = 0.05$). Progenies of trees from the "better sites" (moist, low elevation) grew more rapidly on good planting sites than those from "poorer sites" (dry, high elevation). Progenies of trees from high elevation grew relatively more rapidly, when outplanted at high elevations, than the progenies of low elevation. Four year height growth of progeny from high elevation parents was significantly ($\alpha = 0.05$) greater than that for progenies from low elevation parents. The authors conclude that where topography is highly variable and growing season moisture is a critical factor, selection pressures such as seedling establishment and growth rate are discriminate against the infiltration of genes from trees adapted to radically different,

although adjacent, sites. The authors recommend further investigation of the relation of this phenomena to the establishment and survival of plantations and their subsequent growth.

Longitudinal growth of branches in relation to position in the crown, season, site and spacing in red pine (*Pinus resinosa* Ait.) was analyzed by Forward and Nolan (1964). The pattern of growth appeared to be more closely related to fluctuating environmental conditions than to qualities inherent in the individual tree. The length of the growing season remains relatively stable, while the rate of growth widely fluctuates and depends on the immediate environment. The exact times of beginning and ending growth vary more for the same tree from year to year than from one tree to another in the same year. Time of growth initiation appears related to climatic conditions in a given year.

Rehfeldt and Lester (1966) found that the geographic origin of seed significantly affected shoot elongation and all associated characteristics (except initiation date) of elongation in red pine. They also discovered that the pattern of weekly shoot elongation corresponded more closely to weekly mean temperature than to weekly mean precipitation. Lammas growth also showed a significant effect on the initiation and termination date of shoot elongation.

Height of Jack pine (*Pinus banksiana* Lamb.) from 26 seed sources was studied by King (1966). He found that the mean plantation height at ten years in the field varied from 9.58 feet on the Chippewa National Forest in northern Minnesota to 15.15 feet on the Marinette

County Forest in northeastern Wisconsin. The significant seed source differences ranged from 25% below the plantation mean to 17% above. The author concluded that the selection of "good" Jack pine stands for seed collection (phenotypic selection) appears worthwhile for this species. He also suggested that the selection of tested nonlocal stock will offer even greater improvement.

Joint effects of variation in vigor and frost damage cannot be separated in balsam fir (*Abies balsamea* Mill.) stands (Lester 1970). Patterns of shoot growth, illustrated by periodic measurements in the nursery, indicate that inherent vigor in the phenology of bud development is important in determining the total height of balsam fir in Michigan and Wisconsin (Lester, Jeffers and Wright 1976).

Adams (1973) studied the effects of competition on family growth of loblolly pine (*Pinus taeda* L.) seedlings. An evaluation was made on the effects of crowding on growth. The types and magnitudes of intergenotypic interactions among pairs of families were determined, and the results showed that intergenotypic interactions were both highly variable and pronounced in their effect on early growth. Evidence was also found for precompetition interactions occurring among seedlings surrounded by neighbors of the same family. Despite the fact that this study involved families of outcrossing species in which a considerable amount of variation can be expected, the author detected a high frequency of intergenotypic competitive effects for combinations involving unrelated families. This suggests that such effects are moderately prevalent in natural seedling populations of loblolly pine.

Little was mentioned about the frequency with which the various types of intergenotypic interaction effects occur in natural populations. The results of this study are comparable to results found in predominantly self-pollinating species. Adams concluded therefore, that studies may reveal such interactions to be as important in the population dynamics of outcrossing species as they appear to be in the more selfed plants.

Recently, Townsend and Wright *et al.* (1979) suggested that little interaction exists between seed lot and planting location of red maple (*Acer rubrum* L.). At age five years, they found that the tallest trees at all planting sites were grown from seed of the northcentral and eastcentral parts of the range. Seed collected in New York, Michigan, Wisconsin and northward resulted in trees displaying the most intense autumn color and varying generally from medium to straight stem form. The most crooked stemmed trees were produced from seed obtained in Virginia, Tennessee and southward.

Sorensen (1979) examined variation in growth and phenology of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*) seedlings of eastern Oregon in two common garden studies. Variables associated with distance from the Cascade Range accounted for 80-94% of the growth traits and date of bud set. These variables also accounted for 47% of the variation in the frequency of second flushing but none of the variation in date of bud set in multiple regression equations. He found that the greatest transition in seedling growth and bud set phenology occurred within approximately 250 km of the summit of the

western Cascades. Interaction between distance and elevation within the sampled zone was also significant for growth traits, due to the west-east cline being steeper at higher than lower elevations.

Progenies of ponderosa pine (*Pinus ponderosa* Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev.) grown for twenty years at three elevations show heritable differences in height and diameter growth associated with elevation (Callaham and Liddicoet 1961). Early returns from analysis of altitudinal variation, along an elevational transect in California, indicate middle elevation sources grow best regardless of the elevation of planting site. This seems to contradict the "local seed source is best" idea. At twenty years, inherent differences in growth curves associated with seed source elevation appeared. Trees with low elevation seed parents take off rapidly. Trees with high elevation seed parents start more slowly and seem to be dropping ever farther behind at low elevations. Although the high elevation trees at age twenty did very poorly at the low and mid elevation sites, they grew taller at the high elevation sites than the low elevation sources and nearly as tall as the mid elevation sources. This pattern continued through age 29 (Conkle 1973). Conkle also found that the variance component related to elevation zones contributed more than that for families within zones at the low and middle sites, but not at the high sites. The results revealed the existence of genetically different populations at different elevations. Generally, local seed sources grew best at each planting and the populations demonstrated continuous clinal genetic variation (Callaham and Liddicoet 1961).

Callaham and Hasel (1961) reported that second year ponderosa pine height growth in the nursery was a good predictor for the fifteen year height of planted trees. Rehfeldt (1980) reported strong relationships between population differentiation and elevation in ponderosa pine in southern Idaho. Strong relationships between elevation and population differentiation have also been observed for ponderosa pine in California (Callaham and Liddicoet 1961) and in northern Idaho and western Montana (Madsen and Blake 1977).

Hanover (1963) measured the growth of shoot apices in a 45 year old ponderosa pine provenance test near Priest River, Idaho. Analysis of the measurements led to the following conclusions: 1) nineteen of the races showed phenological, morphological, or physiological variation in six of the characters of interest; 2) the variation described was continuous, although it was not possible to associate an environmental gradient to the pattern; 3) all trees (except the local Kaniksu source) achieved their maximum surge of growth during the same seven day period, and this response closely paralleled temperature fluctuations; 4) simple correlations among the progeny between total seasonal elongation and either beginning date, relative rapidity, or duration of growth were not significant. Correlation between dormant terminal bud length and total seasonal elongation was strong. Bud length was positively correlated with relative rapidity, and relative rapidity was negatively correlated with duration of growth.

One and two year height growth of ponderosa pine was positively correlated with height at age eight, seed size, seed weight and

germination capacity (Wang and Patee 1973). The major sources of variation in seedling height included among stands and among families within each stand. The inverse correlation between seedling height and altitude of the seed origin was found to be highly significant. However, the fastest and slowest growing progeny and stands were all from the broad belt of middle elevations. In a subsequent report, (1974) the authors noted that the difference in height at ages five and eight between stands became increasingly distinct, and the differences within stands among progeny families became increasingly uniform.

Height growth of 71 families of ponderosa pine in seven elevational zone sources varied between seed source zones and between families within zones (Namkoong and Conkle 1976). Differences between elevational zones accounted for a major proportion of the observed variation. Zonal variances were expressed at an early age, and the differences continued, with minor variations, through the 29 year study period. Family variances appear smaller than zonal and environmental variances, and the differences between earlier and later phases were poorly correlated. Sometimes negative correlations existed. The observed growth phases, related to ecological dominance and competition, affected the levels of variance attributable to genetics and environment (Namkoong and Conkle 1976).

Madsen and Blake (1977) reported preliminary results demonstrating significant relationships between genetic variation in several ponderosa pine characteristics and certain environmental variables at the seed source. An analysis of variance for two year height growth

revealed that 71.5% of the total variation was attributed to within and among family (within stand) variation. Significant variation in height growth was also found among stands having the same habitat type and among habitat type groupings. They concluded that the patterns of variation displayed were predominantly clinal.

Correlations and Miscellaneous Factors

Cone serotiny of lodgepole pine (*Pinus contorta* Englm.) on two National Forests was studied by Lotan (1967, 1968). On the Gallatin National Forest near West Yellowstone, Montana, cone serotiny was either pronounced or nonexistent. Most of the trees bore cones that were 90% or more serotinous (closed), or they bore cones that were 90% or more open. Lotan (1967) concluded that even aged stands originating by fire were established by seed cast from closed cones which opened during the fire. Additionally, uneven aged stands became established primarily from open-coned trees over the years. The high percentage of serotinous-coned trees, occurring in fire originated even aged stands, suggests a strong genetic component with selection for the serotinous trait. These trees undoubtedly originated from closed cones in the previous stand.

Results from the Targhee National Forest were similar to those on the Gallatin (Lotan 1968). Trees were considered serotinous-cone bearing if 90% or more of the cones were closed and considered open if 90% or more of the cones were open. A regression of recorded plot data and tree factors explained less than 10% of the variation in percentage of serotinous cones per tree. Elevation and stand age were the two

most obvious statistical contributors to the results of the regression. The effect of stand history was superimposed on all factors.

The mean weight of mature red pine (*Pinus resinosa* Ait.) seed cones varied appreciably in a study by Dickman and Kozlowski (1971). The heaviest cones were generally borne in the middle third of the crown and on second order branches. Regression and correlation analysis revealed that cone volume was positively correlated with the number of full seeds per cone, total dry weight of the seeds per cone, and the number of scales per cone. A less apparent relationship was found between the number of scales per cone and the number of seeds per cone.

At the beginning of the second growing season of red oak (*Quercus rubra* L.), McGee (1974) found that the date of budbreak and rate of seedling development were significantly correlated ($\alpha = 0.05$) with elevation of the acorn source. Date of budbreak and height growth were also found to be significantly correlated ($\alpha = 0.05$) with elevation of the planting site. The budbreak period for the entire study covered a 38 day span. At each planting site, budbreak of the seedlings from the various seed sources occurred over an eleven day period. This study showed conclusively that moving northern red oak acorns from one elevation to another can affect the future phenological performance of the seedlings.

Hamrick and Libby (1972) indicated that white fir (*Abies concolor* (Gord. and Glen.) Lindl.) constitutes a highly variable species whose patterns of genetic variation in a common garden often correlate with the latitude and elevation of the collection site. More recently,

Hamrick (1976) divided the western part of the range into four morphologically distinguishable geographic regions, and demonstrated that within each of the four regions smaller, but more important, differences exist between populations for most of the characteristics measured. Often, this within-region variation correlates with the latitude of the origin. However, in this study, differences in elevation between populations within a region seemed to account for most of the intraregion variation. Furthermore, characteristics concerned with growth were influenced to a greater degree by changes in the elevation of the population than were the characteristics of needle morphology.

Juvenile assessments of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) by Samuel and Johnstone (1979) indicate that selection cannot proceed with any confidence until after 4-6 years of age. Family mean height rankings flip-flop around until the 4th year or so and then are more steadily maintained. The authors concluded that juvenile assessments do not necessarily provide information on family performance in later years.

Khalil and Douglas (1979) used height growth of black spruce (*Picea mariana* Mill.) as the response variable in their analyses. No independent variable was found to correlate with the response variable in a simple linear manner. Only one variable, latitude, occurred alone and was correlated with height growth in the quadratic power. All other independent variables were correlated through interactions with each other. Only four independent variables, out of the 54 tested at the origin of the parent trees, were significantly correlated ($\alpha = 0.05$)

with the four year height growth of black spruce. They include: 1) the square of the latitude; 2) the interaction of longitude and mean precipitation from May to September; 3) the mean number of frost free days and mean number of days during the annual growth period; and 4) the interaction of mean number of frost free days during the annual growth period and the day length on June 21st. These variables were statistically significant ($\alpha = 0.01$).

Morgenstern and Teich (1969) demonstrated that northern provenances of Jack pine (*Pinus banksiana* Lamb.) which were moved 2°-3° latitude southward, often grew taller than in their native habitats, but not as tall as the local or more southerly provenances. In contrast, southern provenances which were moved 1°-2° northward grew better than at their latitudes of origin, and in some instances surpassed the local provenances by 10-20%. Statistically significant ($\alpha = 0.05$) correlations between height growth and latitude of origin occurred in nine of the twelve experiments. Analysis of variance of mean provenance heights at all environments attributed 82% of the observed variation to the environment, only 9% to the provenance effect and 9% to provenance X environment interaction. These results closely agree with the results of King's (1965) study of seed source X environment interactions in Scotch pine (*Pinus sylvestris* L.).

Multiple regression analyses indicated that ponderosa pine (*Pinus ponderosa* Laws.) height was significantly associated with seed source elevation (Callaham and Hasel 1961). About 39% of the variation in fifteen year height could be attributed to heritable genetic

differences between progenies. Seed trees producing relatively large seed which germinate rapidly tended to produce progeny with superior height growth during the second year.

Seed size was determined according to weight in a study by Fowells (1953). He revealed that seed size had a short term effect on survival and growth of trees. Seedling size was positively correlated with seed size for at least three years, and then the strength of the relationship diminishes annually. Seed size was related to seedling size but not to inherent vigor.

Van Deusen (1980) found excellent correlation in ponderosa pine between average tree height at plantation ages five and ten years for the twenty tallest provenances. If trees, recognized from juvenile growth as outstanding growers, will continue as such, substantial time will be saved in the selection of improved trees. A single trait such as ten year height growth or ten year survival does not fully indicate performance. A very few tall trees, or survival of many short ones, requires more information to recommend those provenances as seed collection areas. Fortunately, Van Deusen (1980) found that the best growing sources generally also showed the best survival and least damages by insects, diseases or animals.

Regional Differentiation

Genetic data derived from range-wide provenance tests provided a method for subdividing Scotch pine (*Pinus sylvestris* L.) into geographic races or portions of clines (Ruby and Wright 1976). Delineation of ranges for 20 taxonomic varieties with proven genetic basis resulted.

Four varieties from Michigan and three additional races, not described taxonomically but distinct enough to warrant varietal status, also provided information on geographic distribution and performance. The results indicated significant differences among three varieties from Scandanavia, three from Siberia, six from Central Europe, one from the British Isles and seven from southern Europe and Asia Minor.

Twelve populations of Rocky Mountain Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco.) were compared by Rehfeldt (1974b) to assess local differentiation of populations in northern Idaho. The populations represented north and south aspects at three elevations in each of two drainages. Tests of two year old families growing in two contrasting environments revealed: 1) substantial differentiation that was not associated with the aspect, elevation or drainage from which the seed originated; 2) variation among families within populations; and 3) relatively large components of variance for families associated with date of bud set, number of branches and seedling height.

Statistical analyses of eleven variables in another study of Rocky Mountain Douglas fir (var. *glauca*) suggested a differentiation of populations into three adaptive provinces (Rehfeldt 1979b). The first province included cool environments, regardless of geographic origin. The other two provinces included relatively warm environments from either western Montana or eastern Washington and northern Idaho. Rehfeldt (1979c) found that variation among provinces and among populations within provinces and among trees within populations all contributed to the genetic variance.

There have been at least seven range-wide seed source studies with ponderosa pine (Austin 1932, Moore 1944, Wells 1964a, 1964b, Pearson 1950, Mirov 1957, Squillace and Silen 1962). At least three regional studies exist similar to this one (Conkle 1973, Van Deusen 1974, Wang and Patee 1974). These range-wide studies have delineated two varieties of ponderosa pine in the United States and Canada --- *Pinus ponderosa* Laws. var. *ponderosa* on the Pacific Coast and *Pinus ponderosa* var. *scopulorum* Engelm. in the Rocky Mountains. Korstain (1924) has discussed the differences between these two varieties. Definite inherent silvical characteristics were observed which may be transmitted hereditarily from one generation to another. In other words, climatic forms or varieties with different silvical characteristics should be recognized just as freely as those based on morphological characteristics. A line drawn from southern California to western Montana roughly divides the two varieties. Only one of these range-wide studies (Wells 1964a, 1964b) utilized a replicated design. Wells (1964a) performed a multivariate analysis to outline five major regional "ecotypes" of the species. His "North Plateau Ecotype", which includes the present study area, has not been adequately sampled, so neither its boundaries nor its degree of homogeneity are accurately known.

Read (1980) studied 24 characteristics on seedlings of 80 natural stand seed provenances of ponderosa pine. Analysis using thirteen traits provided a basis for grouping the 80 origins into a pattern of nine geographic clusters. Two of the clusters fit the description of var. *ponderosa*, and the other seven were described as var. *scopulorum*.

These geographic delineations complement previous studies by Wells (1964a, 1964b) and Weidman (1939). Although some minor differences exist between the three studies, mostly due to the numbers of samples and distribution of samples, the basic boundaries agree.

Presently, there are two regional studies on ponderosa pine adjacent to the northern Rocky Mountain area. The first occurs in southern Idaho just south of the Salmon River (the southern boundary of the present study). Wang and Patee (1974) published one, two and eight year old progeny data from this study. Rehfeldt (1980b) continued the study. His data involved eight and eleven year heights, the percent of trees damaged by snow and the percent of trees with straight stems. Analyses of variance revealed population differentiation for height at both ages but not for the percentages of snow damaged or straight stemmed trees. Differences among populations accounted for about 20% of the genetic variance; most of the genetic variance occurred within populations. Multiple regression analyses relating population differentiation to geographic and ecologic variables suggests that elevation of the seed source controls differentiation; latitude and longitude are secondary; habitat types are unimportant. Family heritability estimates on eleven year height range from .37 to .53, implying that genetic gains of about 7% can be expected readily in the eleven year height of progenies from selected families. More recently, Rehfeldt (1980b) in his study of southern Idaho ponderosa pine presented results that attest to potential genetic gains at several levels of tree improvement for ponderosa pine. First, seed transfer

guidelines account for natural adaptation of populations and reduce losses in productivity from maladaptation. The guide lines limit seed transfer to \pm 700 feet elevation, \pm 50 miles latitude and \pm 60 miles longitude. Secondly, a 4% gain in sixteen year height can be obtained by collecting seed from populations of proven genetic potential. Finally, depending on the intensity of selection, gains in height from 8% to 14% can be expected in the next generation from seed orchards developed from selected individuals within selected families. Genetic gains in sixteen year height were related to: 1) seed collections within seed zones; 2) seed collections from selected populations within seed zones; and 3) seed orchards developed after family trials.

The second study, located in the Black Hills, contains a few families from western Montana, but by far most of the other families come from areas east and south of the present study area. Van Deusen (1974) reported on five year old progeny data from this study. When the provenances for ponderosa pine in the northern Great Plains were grouped into geographical clusters, there were statistically significant differences in mean survival and height growth among clusters. Most of the clusters have substantial performance variations among the included provenances (Van Deusen 1980).

Many of the range-wide and regional studies have found adaptive variation (Madsen 1975). However, Squillace and Silen (1962) have shown that seed sources from other geographic areas do not perform well in the Inland Empire.

Seed Zoning

The classification of habitat types and populations can prove quite useful when investigating genetic lines (provenances, races, ecotypes, etc.) which sample natural populations in a heterogeneous forest region. Schotte (1923) related differences in mortality of planted, nonindigenous provenances of Scotch pine to the mean annual temperature of their habitats. Shortly after, a transfer model for predicting effects of seed transfer was devised by Eneroth (1926). Then Langlet (1945) proposed rules for stratifying forest regions into "seed collection" or "provenance" zones.

More recently, the value of stratification has been recognized as a way of reducing genotype X environment interaction components. Genotype X environment interaction results from the failure of genotypes to show the same relative performance in different environments. Interactions between genotype and environment in species is a prerequisite for superiority in the mixture of pure lines or species. Only if different genotypes react differently to different environments can a mixture be superior. These interaction components often become as large or larger than the genetic component of forest species in field tests (King 1965, Morgenstern and Teich 1969). Besides reducing the variance component for genotype X environment interaction, stratification can make the reference environments more homogeneous and thus increase the useful genetic variance (Comstock and Moll 1963). The size of the genotype X environment interaction determines whether special, locally adapted breeds or more generally adapted ones are developed. At the individual

tree level, genotype X environment interactions become the most important factor.

The genotype X environment interaction can be estimated from progeny and provenance trials repeated in different environments (Morgenstern and Teich 1969). Variance components obtained from mean squares provide estimates of genotype X environment interaction for all genotypes as a group. Cockerham (1963) has discussed in depth the various aspects of the estimation of genetic variances. He demonstrated several procedures, depending on the mating design of the experiment. The amount of inbreeding, the relationships of the parent trees, and the number of factors used in the design each have sections in the paper, and some methods of calculating the expected mean squares are also given.

Langlet (1934 and 1936) demonstrated that population diversity corresponds closely to environmental diversity. Based on this, stratification usually follows a clinal response of genotypes to climatic gradients. In concept, most clines are described by fitting regressions of provenance performance to climatic, geographic, or physiographic parameters (Campbell and Sorensen 1978). By using the regression line slope in conjunction with criteria of acceptable adaptation, seed planting zones or provenance transfer rules can be devised (Morgenstern and Roche 1969, Stern 1974, and Campbell 1974).

Two problems warrant consideration before implementing the above procedure. First, which trait or traits should be used as indices of growth and adaptation, because not all traits in populations follow

identical clines (Holzer 1969, Hamrick and Libby 1972). Second, in forest species the pattern of triat response at various levels of an environmental factor (i.e. the response curve) may vary among provenances or ecotypes. Curves may differ in intercept, shape, and placement of the maxima or minima (Jensen and Gatherum 1967, Hermann and Lavender 1968, Lavender and Overton 1972, Sorensen and Ferrell 1973, Campbell and Sugano 1975).

Clines may also be described by fitting estimated genotypic values of populations to regression models. The regression describing a cline may vary because rankings may be influenced by the test environment. This would also affect the choice of the model used in delimiting provenance zones or seed collection zones. Potentially, this problem becomes greatest when estimates result from the "common garden" experiment, especially with only one environment. When using several test plantations the problem may also prove significant (Campbell 1974).

Campbell and Sorensen (1978) revealed clinal patterns of the greatest complexity for warm air and soil temperature test environments of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*). The authors studied seedlings from 40 populations of northwestern Douglas fir in eight nursery bed treatments which contrasted air and soil temperatures. The population samples interacted significantly with soil temperature for growth traits, and with soil and air temperatures combined for phenological traits. Both the complexity and the gradient of the clinal pattern depend on the trait and the specific test environment. The estimate of clinal structure in Douglas fir

proposed by Campbell and Sorensen (1978) suggested more risk of poor survival and shorter height growth, within the northwestern United States, when moving provenances east-west than north-south. This risk increases with elevation of provenances, and the north-south transfers become more critical near the coast than inland. These transfer rules can facilitate delineation of seed collection zones and breeding zones for northwestern Douglas fir.

Genetic variation in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco. var. *menziesii*) has been partitioned into components attributable to parent tree location and to differences among trees within locations (Campbell 1979). Within-location variation appeared more homogeneous within the Lookout Creek watershed of the McKenzie River drainage on the western slope of the Cascade Range in west central Oregon. Between-location variation seemed related to topography, but the patterns of trait variation differed depending on the trait measured. Growth traits exhibited strong gradients with elevation, but the relationship varied depending on position within the watershed. He found a surprisingly large genetic differentiation in Douglas fir within the watershed. Campbell suggested that the topoclinal variation in traits probably resulted from selection as did the large within-location variation. Both kinds of variation result from high selection intensities in the seedling stage; the former to selection by average environmental differences along gradients; the latter to micro-environmental heterogeneity. The combination of high within and between-habitat variation suits a species which episodically colonizes an environment that is extremely heterogeneous in space and time.

Jeffers and Jensen (1980) found grouping plantations and/or grouping seed sources for Jack pine (*Pinus banksiana* Lamb.) in the Lake States unsuccessful mostly due to large differences in plantations. They divided the trees into three groups for survival, height, diameter, and volume per acre. Seed sources from Group 1 (northeastern Minnesota) and Group 3 (southern part of the Jack pine range in Michigan, Minnesota, and Wisconsin) contribute most to the genotype X environment interactions while those in Group 2 (middle latitudes) contribute very little to the interactions. The distance from the seed origin to the planting site apparently accounts for these differences, this distance being least for the middle latitude seed sources. They also found height at age five years an unreliable method for estimating height at age twenty years.

White cedar (*Thuja occidentalis* L.) displays the ability to persist in a wide range of habitats. This characteristic pertains to the wide degree of adaptability possessed by the species. Habeck (1958) collected and transplanted naturally occurring white cedar seedlings from upland and lowland habitats throughout its range in Wisconsin. He also collected seed for germination tests and growth experiments. The results of the transplantation experiment indicated that real differences exist between upland and lowland white cedar. The reasons for the significantly higher survival of upland seedlings was unclear. However, the presence of ecotypes and the relatively better cold adaptation conditions of the upland white cedar was clear.

The percent of germination for stratified seed compared with nonstratified seed showed no significant difference. However, within the stratified seed group, the upland white cedar had a significantly higher percent germination than the lowland seed. Among the nonstratified seed, no significant difference existed between upland and lowland seed. Under natural conditions, seed of both upland and lowland habitats would experience a cold treatment; therefore more importance should be given to the germination results of the stratified seed. The author did not try to explain the cause of the difference; he only indicated its presence and concluded that ecotypes exist within white cedar in Wisconsin.

Western white pine (*Pinus monticola* Dougl.) exhibited genetic adaptation along environmental gradients (Barnes 1967). Racial differences, typically clinal in nature, were associated with changes throughout a large geographic area. Local differences in western white pine populations seemed associated with elevation and aspect. Barnes found that height growth of offspring from high elevation female parents was significantly less than that of progenies from low elevation female parents when grown at low and mid elevation plantations. These observations constituted preliminary findings and more time is needed for progeny testing to determine any significant and predictable association of growth rate and other traits with elevation. Such tests could also determine whether the pattern of genetic variation seems more or less continuous, discontinuous or random.

The results of a western white pine study by Hanover and Barnes (1969) illustrated the desirability of using as many parents as possible, and choosing the parents at random from a population, so that heritability estimates will be unbiased. This study resulted in relatively small but repeatable additive genetic components in white pine seedling height growth. The high individual tree variation undoubtedly allows this species to adapt to new environments or changes in the current one. Some additive gene effects on growth rate have been demonstrated in this and other studies. For practical purposes, however, the present need is for measures of relative stability of growth rates in known populations over a range of environments. The authors concluded that information of this type will allow the concept of heritability to contribute more to accurate prediction of genetic gains in long-term tree breeding programs.

In a study of western white pine in northern Idaho, Steinhoff (1979) concluded that only two seed zones need differentiation. The main or low zone should include all the area below 1375 m excluding a limited area of very severe sites between 1250 m and 1375 m. All the area above 1375 m and the limited area, between 1250 m and 1375 m, of very severe sites, comprise the second or high zone. These results provide only guidelines, because factors other than elevation, such as the growth and form characteristics desired and the survival rate of the offspring, must be considered in selection of seed trees.

Townsend *et al.* (1972), Rehfeldt (1978) and Steinhoff (1979) suggested that nearly all the genetic variability in western white

pine, which might be utilized in a tree improvement program, relates to the differences among individual trees within stands rather than to differences between stands, elevational zones or geographic areas. When stand or area differences showed significance, there did not appear to be a pattern to the variation. Steinhoff (1979) concluded that western white pine contains a high degree of variability, but most of the variation relates to differences among offspring of a single tree or among trees in a stand. Although differences between stands, elevational zones or geographic areas were sometimes significant, the proportion of the variance attributable to these sources usually proved smaller than that for trees within stands. Therefore, it appears western white pine has become adapted to environmental heterogeneity by means of phenotypic plasticity rather than by adaptive differentiation (Rehfeldt 1978). Although individual white pines are heterozygous and populations are heterogeneous, selection apparently has not acted on the genetic variability to produce populations of different adaptive norms (Steinhoff 1979).

If population sample differences, exposed by "artificial" tests, relate to environmental differences at the population origin, it indicates that these differences are adaptively significant. For example, confidence can be enhanced if genetic variation as well as the genotype X environment interactions show clinal structures. Such a relationship implies that response curve shapes differ among population samples, and that curve shapes change along clinal gradients. This complex structure of genetic variation is difficult to justify except as a

refined adjustment of populations to natural selection (Campbell and Sorensen 1978).

The adaptive strategy and the genetic system have evolved in the natural environment. Different species face different levels of environmental heterogeneity. Consequently, different species have different genetic systems, adaptive strategies and seed zones.

Seed zones of a particular species must reflect its system of genetic variability and must be consistent with its adaptive strategy. Once the genetic system is understood and the adaptive strategy disclosed, the genetic basis for tree improvement becomes known and seed planting zones become evident (Campbell and Sorensen 1978).

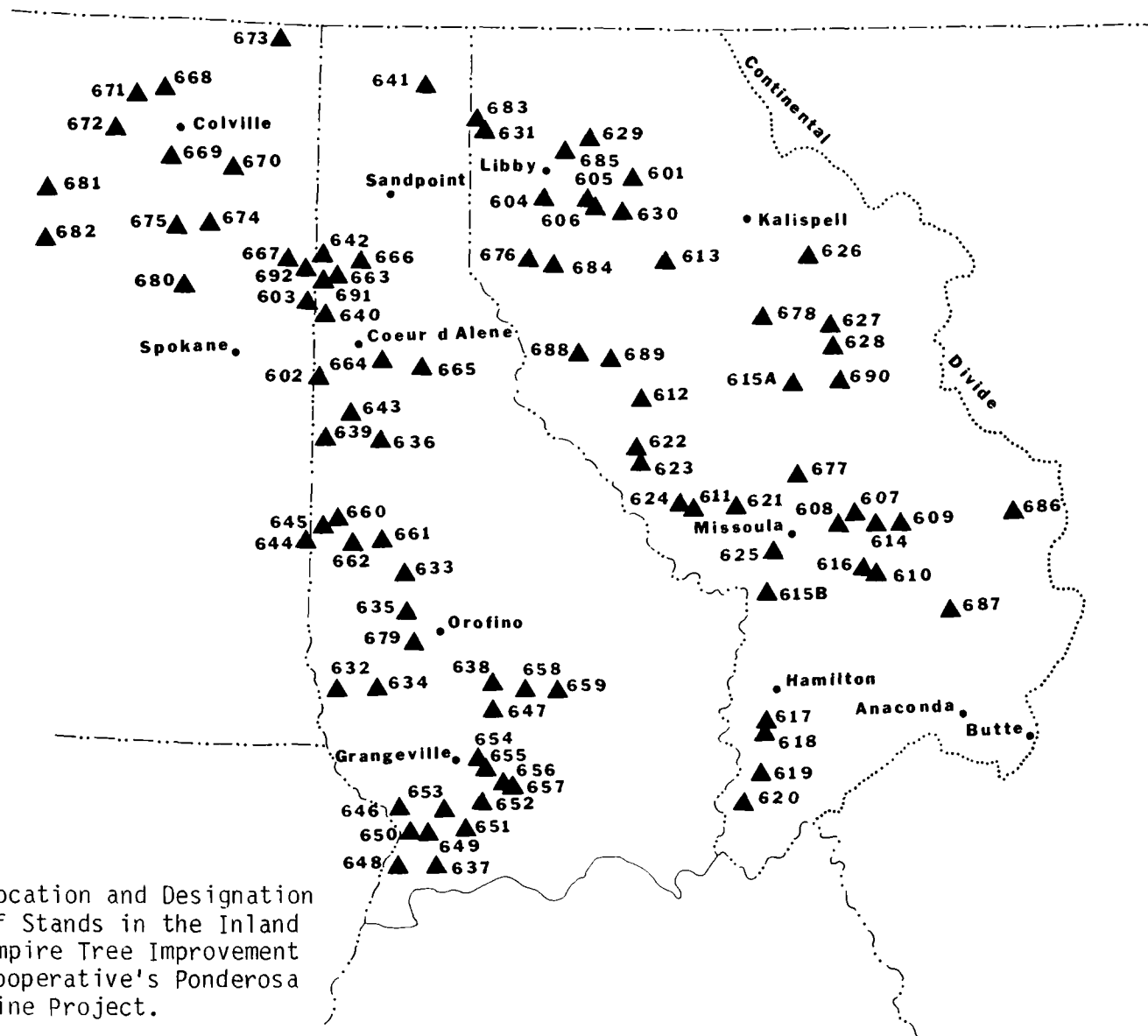
METHODS

History

Members of the Inland Empire Tree Improvement Cooperative made the seed collections for this project. The area of seed collection extends from the Canadian border south to the Salmon River and from the Okanagan River east to the Continental Divide (Figure 2). The cooperators subjectively chose 93 wild stands of ponderosa pine from this area on the basis of their above average growth performance.

Within these selected wild stands, 434 parent trees were chosen. They displayed phenotypically superior growth traits which indicate promise, but not proof, of genetic superiority. Open-pollinated seed collections from these trees were made from 1968 through 1971. Seed from each parent tree was kept separate from other seed lots and identified as a half-sib family. A random seed collection (bulk or control) was also made from each stand. In 42 of the 93 stands, the seed was obtained from squirrel caches or trees of average phenotype. For the remaining 51 stands, a random collection was synthesized using seed from the selected parent trees in those stands. The "bulk" families provide a basis for comparisons between average and selected trees, as well as performance across different environments.

Seeds from the collections were sown by family in a randomized complete block design at the USFS nursery in Coeur d'Alene, Idaho during May of 1972. The seedlings grew undisturbed for two years. In April 1975, (the third growing season), the seedlings were lifted and



permanently transplanted into one of eight test plantations whose locations cover a wide variety of environmental situations (Appendix B).

A randomized complete block design was used again for the out-plantings at each location. Four seedlings from the same family were planted in 10 ft. X 10 ft. spacing to form a family plot. Half-sib family plots were established in each of five blocks to form a test plantation at a particular geographic location. Also, each plantation contains between two and ten (depending on the site) randomized block plantings of the "bulk" collections from the various stands. In 1976, four year height measurements were taken by the cooperator responsible for each plantation to use as base line figures in the future.

Field Procedures

Dale Coffen at the Intermountain Forest and Range Experiment Station in Moscow, Idaho helped design the data forms to facilitate simple and straightforward recording (Appendix C). The data are organized according to rows identified within each plantation. The following information was included on each form: the plantation number, the row and column, the family identification number, the year planted, the nursery code, and the 1976 height. Columns were then provided for the 1978 and 1979 height measurements, a diameter measurement, a series of damage indices, and a space for remarks.

Trees which exhibited superior volume production were selected on the basis of the indirect indicators, height and diameter. Those indicators are more highly correlated with volume production, therefore

other growth traits including needle length, fiber content, root spread, crown form or crown density were not considered. Only height and diameter are considered dependent variables because of their relationship to fitness and volume production and their importance in the analysis of changes in growth patterns.

Originally, only 1979 height measurements were to be taken, but because of extensive frost damage on the Montana plantations, 1978 height measurements were included for consistency. This permitted comparisons across all plantations for height change from 1976 to 1978 and from 1976 to 1979 on those plantations that remained unaffected by the severe winter damage.

The Elijah plantation is not included in this study because of previous circumstances which led to the restocking of the entire plantation in the spring of 1979. When these new trees reach their seventh growing season, they may be measured and then compared to the results of the other seven plantations. The remainder of this study includes only seven of the eight original test plantations.

Approximately 50,000 height measurements were made after growth cessation during the summer of 1979 on the half-sib families. In addition, another 25,000 measurements were taken on the random stand (bulk) collection progeny. A two meter stick was constructed to facilitate these height measurements which were made to the nearest centimeter (± 1 cm). Participants in the cooperative provided field assistants to help record the data.

The meter stick was placed on the ground at the base of the tree. Total height for 1978 was measured from the ground to the preceding year's growth node. Total height for 1979 was measured from the ground to the base of the terminal bud. This actually measures seven years of growth. The dominant lateral was measured on those progeny that had terminal bud or leader damage. At this age it is very likely that the trees will only suffer a setback in growth for a few years, and 100 years from now the ill effects will hardly, if at all, be noticeable. Base measurements for all trees in the progeny areas were subtracted from and compared to their respective new measurements. These differences display changes in height over time and indicate family performance on a particular site.

Height and diameter measurements provided the basis for estimating phenotypic variation. The difference in observed growth for one family planted across all locations represents environmental variation, while the difference between families planted at the same location estimates genetic variation. In these test plantations the genetic component was evaluated, not by comparing the growth of one tree against another in the varied environment of a wild stand, but rather by comparing the growth of a group of related trees against another group of related trees in a uniform environment.

Base line diameter measurements, using outside diameter calipers and recording to the nearest millimeter (± 1 mm), were taken at a height of 30 cm above the ground for future reference and analyses. Trees less than 30 cm in height were not included.

A damage index was derived and recorded which assessed winter damage at the Montana plantations. The code was based on one suggested by Warren Roberts at the Condon plantation and proved very useful (Appendix D).

Other recorded general damages that occurred in varying degrees at different plantations include: western gall rust, mechanical damage, competition from grasses and other vegetation, rodents (porcupines, gophers, ground squirrels and mice), needle cast, insects (needle miner, western pine shoot borer, pine tip moth), forking, browsing by big game, trampling by cattle and summer drought. Codes were standardized for each of these damages (Appendix D).

All data recorded were then entered into the computer and stored in files on disk and magnetic tape for future reference and utilization.

Analyses

An analysis of variance (ANOVA) is appropriate for estimating variance components when an equal number of observations per subclass exists. However, when an unequal number of observations per subclass prevails regression techniques are employed if the imbalance is not severe, i.e., 30-40 missing observations. If a very severe imbalance exists, i.e., several hundred missing observations, a preferable method is the ANOVA with a proportional number of observations per subclass as discussed by Bancroft (1968).

Analysis of variance for multiple classified data usually involves an equal number of observations for each subclass. Using the standard model assumptions, this leads to a relatively simple analysis of the

data and straightforward inference procedures. However, if unequal numbers of observations in the subclass exist, the analysis and inference procedures become more complicated (David 1951 and Grossman 1970). In the case of a two-way classification with unequal frequencies in the subclasses, the complete model includes:

$$Y_{ijk} = \mu + A_i + B_j + (AB)_{ij} + \epsilon_{ijk}$$

where:

A_i = Block effect ($i = 1, 2, 3, 4, \text{ or } 5$)

B_j = Family effect ($j = 1, . . . , t$)

$(AB)_{ij}$ = Interaction effect

ϵ_{ijk} = Error ($k = 1, 2, 3, \text{ or } 4$)

This general model provides unbiased estimates. Zuuring (1980) wrote the computer programs in FORTRAN for the Dec-20 computer at the University of Montana.

In this study, treatment combination frequencies resulted in unequal observations at the family level due to mortality and missing observations. Only selected families could be used at each plantation because of unequal numbers at the two levels of the analysis, i.e., unequal numbers of blocks utilized and unequal numbers of families represented at each plantation. This influences the variance components estimated and the expected mean squares (EMS). Some of the data was eliminated to achieve proportionality in the subclasses. The interaction and each main effect could then be calculated independently for testing their significance.

For each plantation the data was visually scanned to determine the distribution of missing observations and to decide which families and blocks to use in the analysis. Any family that had zero observations in one or more blocks was eliminated from the analysis at that plantation. The Montana plantations contain a large number of missing observations. Therefore, two separate analyses were performed on these four plantations. The first eliminated families to retain all five blocks in the design. The second eliminated blocks to retain the maximum number of families. A minimum of two blocks was necessary for any variation to be evident at this level. For consistency, the number of families included comprised 90% or more of the total number planted. For the Idaho plantations only one analysis was necessary, because all five blocks could be used and still retain 90% or more of the families planted.

All of the analyses used proportional numbers of observations within each family. For each plantation, the elimination of seedlings was such that the number of seedlings remaining in each of the blocks retained was constant within each family. For example, if the numbers of seedlings for a family per block in blocks 1 through 5 respectively are 3, 2, 2, 3, 2, then random elimination of one seedling from block 1 and one seedling from block 4 "balances" that particular family at that plantation. Another plantation, for example, may only use blocks 2, 4, and 5 in the analyses. If a family then has 3, 4, and 1 observations respectively in the three blocks, then random elimination of two seedlings in block 2 and three seedlings in block 4 "balances" that

particular family at that plantation. A different family may use a constant of three observations across all blocks retained, thus unequal observations occurred between families within a plantation.

A two-way analysis of variance by block and family was computed separately for seven year total height at each of the seven plantations. From the two-way analysis of variance at each plantation, an estimate of the "true" variation among sources was obtained as a "component of variance" after the allowance for random variation (Snedecor and Cochran 1968). The form of the analysis of variance and expected mean squares (Table 1) follows the example of Wright (1963).

Although the sums of squares computed easily, a difficulty arose in the expected mean squares for the main effects and the interaction due to the unequal numbers of observations in the subclasses. Thus, the F-tests were more difficult to calculate. The only straightforward F-test of significance applicable was the block X family interaction. To calculate significance for the main effects (blocks and families), an approximate method had to be used. The method used in this study was the Satterthwaite-Cochran approximation. For a detailed description of these procedures, consult Bancroft (1968).

Heritability Estimates

Two types of heritability, broad-sense and narrow-sense, yield valuable information. Broad-sense heritability considers genotype as a unit in relation to the environment. Heritability in the narrow-sense expresses the fraction of the phenotypic differences between parents which one expects to recover in the offspring. The design gives a

practical interpretation to heritability (Hanson 1963). Thus, heritability in the broad-sense considers total genetic variability in relation to the phenotypic variability, while heritability in the narrow-sense considers only the additive portion of the genetic variability in relation to the total phenotypic variability.

Only additive genetic variability can be estimated in an open-pollinated progeny test such as this one. Therefore, heritability can only be estimated on a narrow-sense basis. Since vigor characters in trees appear primarily controlled by additive genes, the use of narrow-sense heritability poses no restriction (Madsen 1975). To make this estimate, an attempt was made to control environmental variation by reducing it physically and discounting it statistically.

Statistically, heritability (h^2) equals the ratio of the total additive genetic variance (σ_f^2) to the total phenotypic variance (σ_w^2).

Thus:

$$h^2 = \frac{\text{additive genetic variation}}{\text{total phenotypic variation}}$$

The concept of heritability in a selection unit can be used as a practical measure because the denominator is the phenotypic variance of the unit (Hanson 1963).

If it is assumed that all the individuals within families are half-sibs then the genetic variation derived from the test will be 1/4 of the additive genetic variance (σ_f^2) (Wright 1921). Thus, heritability estimates should correctly contain $4\sigma_f^2$ in the numerator (Madsen 1975).

The previous equation then becomes:

$$h^2 = \frac{\sigma_f^2}{.25(\sigma_w^2 + \sigma_f^2)} = \frac{4\sigma_f^2}{\sigma_w^2 + \sigma_f^2}$$

where:

h^2 = heritability estimate

σ_f^2 = additive genetic variation

σ_w^2 = environmental variation

Difficulties of estimating genetic components of variance and heritability using open-pollinated seeds have been discussed by a number of researchers (Namkoong 1966, Squillace 1974, and others). Three main items contribute to these difficulties: 1) relatedness of the seed parent with its pollinators; 2) relatedness of the pollinators; and 3) small numbers of pollinators for many seeds. Genetic variance and heritability estimates should also take into account any correlation that may occur among seed parents and among individuals within families when using open-pollinated trees (Squillace 1974). Additive genetic variance decreases with increasing correlation among offspring within families and increases with increasing correlations among parents. These correlations affect heritability estimates in the same manner.

In this study, family height growth heritability estimates were computed for each plantation. From the analyses of variance at each plantation, variance components were used to calculate family heritability from the following equation:

$$h^2 = \frac{4\sigma_B^2}{\sigma_{\text{error}}^2 + \sigma_{AB}^2 + \sigma_B^2}$$

where:

σ_B^2 = additive genetic variance

σ_{AB}^2 = interaction variance

σ_{error}^2 = error variance

$\sigma_{\text{error}}^2 + \sigma_{AB}^2 + \sigma_B^2$ = total phenotypic variance

Two heritability estimates were calculated on each of the Montana plantations. The first one used all 5 blocks regardless of the number of families that became included. The second used 90% or more of the families represented at each location by eliminating entire blocks as necessary. Due to mortality and missing data, between 8.14% and 10.29% of the families were eliminated from the analysis of variance calculations and subsequent heritability estimates.

Multiple Comparison Procedures

The null hypothesis of this study was that no significant differences exist between seven year family mean heights within each plantation. Once the ANOVA established that significant differences do exist and the hypothesis was rejected, several methods became available for pair-wise comparisons of the means. All methods make use of Snedecor's F-distribution (Snedecor 1956). The multiple comparison methods in common use include: the Least Significant Difference (LSD), Scheffe's method (S), Student-Newman-Keuls' method (S-N-K), Tukey's Honestly Significant Difference (T-HSD) and Duncan's method (D). Each procedure is based on a particular set of assumptions and is usually effective for a specific purpose. Unfortunately, these tests vary considerably

in their ability to distinguish significant differences (sensitivity) among means.

In general, all the above mentioned multiple comparison methods, except Scheffe's based on the special ordinary studentized range table, are exact only for equal numbers in the groups and for means that have not been adjusted by covariance. Scheffe's method, in contrast, produces exact results for means based on unequal as well as equal sample sizes and means that have been adjusted by linear covariance. The difficulty arises in the other procedures because they require equal variances and independence of the population means.

Scheffe's method (Scheffe 1958) is on one end of what could be considered a spectrum. This very general method may be used to test a general hypothesis or to set confidence limits of a linear function. Usually the generality of this method causes a small number of differences declared significant as compared to the multiple range comparison procedures based on the studentized range. For the purposes of this study, Scheffe's "S" test produces fewer significant differences than would be expected. The procedure requires large discrepancies to establish significant differences between means and yields results too conservative for meaningful interpretation.

At the other end of this spectrum is the very liberal LSD method. This procedure can be modified for use when the sample means are computed from unequal sample sizes. This procedure uses the pooled sum of squares of deviations divided by the pooled degrees of freedom. A single chosen pair of independent family means may be compared in an

optimum manner by an ordinary t-test, the LSD method. However, this method yields a relatively high experimental error (Hartley 1946). As a consequence, the test is not sensitive enough. Many more significant differences result than would normally be expected. This method is not usually recommended for multiple comparisons of all pairs of population means. When several comparisons become necessary, all of the multiple comparisons cannot be independent; procedures other than the simple LSD method, valid for independent comparisons, must be considered.

Intermediate results can be obtained from the Student-Newman-Keuls procedure, Tukey's Honestly Significant Difference and Duncan's procedure (Panaik 1950). All three of these procedures are sensitive to α and the degrees of freedom (d.f.).

In testing differences among mean heights, the most sensitive is the S-N-K test (Steele and Torrie 1960). However, this procedure does not have the approximate character of the other two procedures. It is less powerful and more conservative in the number of differences declared significant. A disadvantage of this procedure lies in its power of testing the differences between all pairs of means, because the magnitudes of the other true means definitely influence the results (Bancroft 1968). Also, when the means are ranked sequentially, the S-N-K method does not account for the number of means skipped over between the two compared.

When the means are ranked sequentially, both Tukey's and Duncan's procedures account for the number of means skipped over between the two means being compared. For example, if 20 means are compared pair-wise,

different critical values will result by comparing the means ranked 1 and 10 and the means ranked 1 and 18, because a different number of means have been skipped.

Using Tukey's pair-wise comparison, each family is tested against every other family in a plantation, thus yielding intermediate results. Tukey's procedure has been shown (Bancroft 1968) to control the experimental error at a desired level. This procedure becomes useful in situations in which the primary emphasis is on the use of the experiment as a whole in determining significance of the pairs of population means, or in setting confidence intervals for differences in population means.

Next to the LSD method, Duncan's procedure is expected, in general, to be sensitive in declaring a relatively large number of differences as significant (Duncan 1955). The problem with Duncan's procedure rests with the unequal numbers to perform the ANOVA. However, since a balanced ANOVA was used, Duncan's procedure could be modified. There appears to be no method of modifying the S-N-K, and T-HSD procedures to yield exact multiple comparisons for all pairs of population means for unequal sample sizes (Steele and Torrie 1960). For these reasons, a modified Duncan procedure was used in this study which yielded intermediate results.

RESULTS AND DISCUSSION

A question often neglected in studies of geographic variation is whether differences exist between populations in terms of total amounts of genetic variation. Factors most likely to affect levels of genetic variation in large populations are selection intensities, gene flow and environmental heterogeneity within the sampled area. Increased selection intensities, reduced gene flow, and environmental uniformity create reduced levels of genetic variation. Thus, marginal and isolated populations are expected to have less variation than centrally located populations (Hamrick 1976). It appears that all populations have similar levels of genetic variation. Evidently the combined effects of selection, gene flow and environmental heterogeneity are roughly equivalent for all populations of forest species studied (Libby 1973). When selection culls from many genotypes, the genotypes probably reflect rather closely the environment in which they evolved. Genetic differentiation is promoted when coefficients of selection, acting in populations from contrasting environments, are greater than the rates of migration between populations. The effects of directional selection which would act to reduce within-population variation may be counteracted by the effects of local microhabitat selection which tends to maintain genetic variation within populations. Bradshaw (1959) explains the positive correlation between selection intensity and variation by possible adaptation to microhabitats. A large open-pollinated progeny test involving hundreds of families can have substantial selection intensity.

Source related variation depends on the test environment as well as on the trait (Campbell and Sorensen 1978). A test plantation provides a uniform environment where the genetic worth of a sibling family can freely express itself. Any single test environment exposes only part of the population's genetic variation and presumably only part of its differentiation. The use of the common environment method has a deficiency in that the elimination of environmentally imposed variation may obscure genetically determined differences in the capacity for reacting to special environments. This is particularly dangerous when the purpose is not merely to observe morphological differences but to test physiological responses. Another problem is that while the test environment will suppress some environmentally induced characteristics, others may be evoked which were never expressed in natural habitats. Fortunately, this project has established eight test plantations in varying geographical and ecological situations throughout the study area. Thus, genotype X environment interactions can be observed closely throughout development.

A compromise exists in most species between fitness for the present environment and the flexibility which enables adaptation to changing environments. The progeny of a given family grown in a test plantation may be interpreted as a sample of genotypes that the family can produce. But, of course, not all of these progeny would survive in that family's native environment. Thus, progeny tests can give a good estimate of the total variation component in families (flexibility). However, they do not give as much information about the adaptive characters, related

to native environments (fitness), as they could. Progeny tests, in addition to yielding valuable genetic information such as heritability estimates and patterns of adaptive variation, also must produce large numbers of seedlings for outplanting and future study.

Most forest species contain a large amount of variability, both across their native range and from one individual tree to another within the same stand. Ponderosa pine contains sizeable variation, not only between populations but also within each population sample. The majority of this variability has been observed within open-pollinated families. The mechanism for maintaining this variation with natural selection is not obvious, but may be related to high levels of migration and gene exchange found within the species, combined with microhabitat selection. The large genetic variability and ample seed supply of ponderosa pine provides excellent opportunities for the chance fitting of genotypes with microenvironments to which they are optimally preadapted.

The phenotype reflects nongenetic as well as genetic influences on development. Furthermore, the effects of genotype and environment depend on one another. The phenotypic response to a change in environment differs for all genotypes; the consequences of variation in genotype depend on environmental factors. These interplay effects, of genetic and nongenetic variables, on development is termed the genotype X environment interaction. An obvious and important effect of genotype X environment interactions is a reduction in the correlation between phenotype and genotype with the result that valid inferences become more complicated.

For highly adapted, special kinds of environments the genotype X environment interaction should be large. By contrast, this interaction should be smaller for a broad spectrum of environments (Comstock and Moll 1963). A genotype contributing very little to the interaction, by showing a response similar to the mean of all genotypes, represents a wide ecological range. The purpose of the analysis of variance is to isolate all components of variation, genetic and nongenetic.

An analysis of variance (ANOVA) was computed for seven year total height at each plantation. Results for the Idaho plantations (Table 2) were computed using complete five block representation and included 90% or more of the number of families planted. Presumably 90% of the families provides an adequate sample for estimating variance components. Therefore, to maintain 90% or more of the families at the Montana plantations for the ANOVA, some of the blocks were eliminated from the analysis (Table 3). A minimum of two blocks was required to show any variation at this level. In addition, for the sake of comparison, an ANOVA was computed for the Montana plantations using all five blocks (Table 4).

Calculated F-values by source of variation resulted in significant differences between blocks, families and the block X family interaction at each location (Table 5). The calculations for family significance followed standard procedures, and the calculations for block significance followed the Satterthwaite-Cochran approximation procedure.

Almost all of the sources were statistically significant ($\alpha = 0.01$). There were four exceptions to this, all at the block level.

Table 1. Form of the analysis of variance and expected mean squares.

SOURCE OF VARIANCE	EXPECTED MEAN SQUARES ²
A (Block)	$\sigma^2 + K_1 \sigma_{AB}^2 + K_2 \sigma_A^2$
B (Family)	$\sigma^2 + K_3 \sigma_{AB}^2 + K_4 \sigma_B^2$
AB (Block/Family)	$\sigma^2 + K_5 \sigma_{AB}^2$
Residual ¹	σ^2

¹ Contains all sources of variation involving interactions of replication

² Where:

	<u>Rye Creek</u>	<u>Wolf Creek</u>	<u>Condon</u>	<u>Lubrecht</u>	<u>Meadow Creek</u>	<u>Tensed</u>	<u>Lone Mt.</u>
K ₁ =	0.3119	0.3051	0.3025	0.3031	0.1586	0.2903	0.2674
K ₂ =	225.0000	213.0000	498.0000	395.0000	297.0000	480.0000	540.0000
K ₃ =	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
K ₄ =	5.6882	7.9511	5.3516	6.5060	17.0597	11.1044	12.3792
K ₅ =	2.8441	1.9878	2.6758	2.1687	3.4119	2.2209	2.4758

Note: See Appendix E for calculations of the coefficients.

Table 2. Results of analysis of variance of seven year height for each Idaho plantation using complete block representation and 90% or more of the families planted.

Source	<u>Meadow Creek</u>			<u>Tensed</u>			<u>Lone Mountain</u>		
	Degrees of Freedom ¹	Mean Squares	σ^2 ²	Degrees of Freedom	Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2
A (Block)	4	6693	20	4	3234	3	4	9588	15
B (Family)	86	3399	154	215	4913	320	217	5553	317
AB (Block X Family)	344	1397	186	860	2921	703	868	2522	360
Residual ³	1050	763	763	1320	1359	1359	1610	1631	1631

¹ Families had to be omitted which did not contain trees in all 5 blocks in such a manner that proportional subclass numbers were achieved.

² Variance components (σ^2) were derived according to Table 1.

³ Contains all sources of variation involving the interactions of replicates with the main effects and their first order interactions.

Table 3. Results of analysis of variance of seven year height for each Montana plantation using 90% or more of the families planted.

Source	<u>Rye Creek</u>			<u>Wolf Creek</u>			<u>Condon</u>			<u>Lubrecht</u>		
	Degrees of Freedom	1 Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2
A (Block)	1	2934	12	3	715	0	1	1441	1	2	4181	8
B (Family)	78	560	51	106	1209	66	185	1929	202	181	1549	119
AB (Block X Family)	78	532	91	318	859	88	185	1205	133	362	1092	147
Residual ³	292	272	272	424	685	685	624	848	848	639	773	773

¹ Blocks and families were dropped in such a manner that proportionate subclass numbers were achieved.

² Variance components (σ^2) were derived according to Table 1.

³ Contains all sources of variation involving the interactions of replicates with the main effects and their first order interactions.

Table 4. Results of analysis of variance of seven year height for each Montana plantation using complete block representation.

Source	<u>Rye Creek</u>			<u>Wolf Creek</u>			<u>Condon</u>			<u>Lubrecht</u>		
	Degrees of Freedom	1 Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2	Degrees of Freedom	Mean Squares	σ^2
A (Block)	4	438	1	4	5265	30	4	45083	267	4	8689	26
B (Family)	49	683	31	92	1361	86	90	2053	140	156	1843	113
AB (Block X Family)	196	389	13	368	888	141	356	1020	137	660	1022	120
Residual ³	265	363	363	295	657	657	380	767	767	700	801	801

¹ Families had to be omitted which did not contain trees in all 5 blocks in such a manner that proportionate subclass numbers were achieved.

² Variance components (σ^2) were derived according to Table 1.

³ Contains all sources of variation involving the interactions of replicates with the main effects and their first order interactions.

Table 5. Degrees of freedom and calculated F-values by source of variation for seven year height at each of seven plantations.

Source	Rye Creek		Wolf Creek		Condon		Lubrecht		Meadow		Tensed		Lone Mt.	
	df	F-value	df	F-value	df	F-value	df	F-value	df	F-value	df	F-value	df	F-value
A (Block) ¹	1	8.98*	2	1.01	1	1.56	2	4.63*	4	8.13*	4	1.96	4	5.13*
B (Family) ²	78	2.06*	106	1.76*	185	2.28*	181	2.00*	86	4.46*	215	3.62*	217	3.40*
AB (Block X Family)	78	1.96*	318	1.25*	185	1.42*	362	1.41*	344	1.83*	860	2.15*	868	1.55*
A (Block) ¹	4	1.18	4	6.79*	4	47.77*	4	9.11*						
B (Family) ²	49	1.88*	92	2.07*	89	2.68*	165	2.30*						
AB (Block X Family)	196	1.07*	368	1.35*	356	1.33*	660	1.28*						

¹ Calculations followed Satterthwaite-Cochran procedure (Bancroft 1968).

² Calculations followed the Standard Procedure (Bancroft 1968).

* Statistically significant at $\alpha = 0.01$.

** Statistically significant at $\alpha = 0.05$.

Several reasons explain the results. First, the block source at Rye Creek using all five blocks in the analysis was confounded by the lack of observations at the family level. Only 57% of the families planted could be used for the analysis. Two other plantations, Condon and Wolf Creek, had nonsignificant F-values for the analysis using 90% or more of the families planted. These results were confounded by the lack of blocks in the ANOVA. Blocks in this analysis were eliminated to maintain families. The fourth nonsignificant F-value occurred at the Tensed plantation. Tensed was the most uniform planting site in this study. Apparently the design was not sensitive enough to detect the natural variability of the site. Single tree plots randomly distributed could have been used at this location.

A modified Duncan procedure was used to test differences among treatment means. Families were ranked (tallest to shortest) according to seven year total height within each plantation. After computing the critical values for an extended multiple range table, significant differences were obvious between mean total heights of families within plantations. Each plantation had different rankings and different contrasts.

Practically interpreted, the results imply that genetic gains in tree improvement projects will be highest when using family selection. Indeed, family selection in this entire project has been determined to yield two and one-half times more genetic gain, with all environmental factors considered, than nonfamily selection (Keegan 1976). However,

the project must be large or the selection intensities kept low to provide for genetic diversity in the planting stock for individual seed zones.

The concept of heritability originated as an attempt to describe whether differences actually observed between individuals arose from the differences in the genetic make-up of those individuals or resulted from different environmental forces. Hanson (1963) defines heritability as "the portion of the observed variance for which differences in heredity are responsible". Heritability is the degree to which a character is influenced by heredity as compared to environmental factors. High heritability estimates indicate strong genetic control over a characteristic, and means the phenotype represents an expression of the genotype. The nature of the genetic variability defined, the experimental units considered and the inference population assumed will each affect the heritability statement made for a particular characteristic. Heritability statements depend on the restrictions made for the definition and the reference unit used to determine a measure (Namkoong 1966). For quantitative measures in plant work, a plant, a field plot, replicated field plots in one environment or replicated field plots in two or more environments may be considered as the reference unit. Each reference unit will affect the heritability statement made. Most plants are not selected on the basis of their individual performance, although in some tree improvement programs an estimate of heritability provides useful applications (Duffield 1963).

Heritability has value primarily as a method of quantifying the concept of whether progress from selection for a plant character is relatively easy or difficult to make in a breeding program. Heritability gives a numerical description to the rating of a series of characters and their response to selection (Halloran 1975). Heritability estimates should relate only to the population, trait and environment for which the value was determined, because large variation in heritability estimates have been found in other forest tree species.

Naturally outcrossing tree species are highly heterozygous and commonly show patterns of natural variation that include varying degrees of phenotypic plasticity and genotype X environment interactions. Phenotypic plasticity is usually insufficient to preadapt individuals to all local environments due to limitations in physical processes. These phenomena have a genetic basis and represent nonadditivity in the derivation of narrow-sense heritability estimates.

Results of Squillace (1974) suggest that genetic correlations under open-pollinated conditions usually exceeds the .25 figure commonly used for half-sib correlation. The assumption of a .25 correlation causes an overestimate of the genetic variance and of the heritability. If, for example, the genetic correlation among individuals within families is actually .30, the estimate of additive genetic variance should be $\sigma_f^2/.30$ instead of $\sigma_f^2/.25$. This false assumption could clearly overestimate the genetic variance and thus the heritability.

Genetic correlations that may occur among the parents also affect estimates of these parameters, usually causing underestimates. Over a range of correlations among parents and among their offspring, the two opposing factors usually result in a net overestimate of the genetic variance and heritability. The overestimate usually remains small if the seed parents are correlated but can be appreciable if they are uncorrelated. Biases can be removed if approximate estimates of the degree of selfing are known (Squillace 1974).

In situations of intermediate gene frequencies, small levels of dominance and few males per seed tree family, the genetic variance estimates will almost always be biased upwards (Namkoong 1966). Therefore, average genetic correlations in open-pollinated families will usually give results higher than the 1/4 accepted for half-sibs. Squillace (1974) has devised tables to adjust for these difficulties. Sorensen and Miles (1974) derived an inbreeding estimate for ponderosa pine of 11.3%. Using this value, the heritability estimates calculated for this study should be accurate within 1%.

Two narrow-sense heritability estimates were calculated at each Montana plantation from the variance components of the ANOVA. The first included 90% or more of the families planted regardless of the number of blocks required to achieve this percent. The second shows the effects of missing data on statistical results by sacrificing families to utilize the complete block representation. Only one heritability estimate was computed for each Idaho plantation (Table 6). Estimates computed apply only to the seven year total height. Complete block

Table 6. Narrow-sense heritability estimates for each plantation as calculated from the ANOVA¹.

$$h^2 = \frac{4 (\text{var. B})}{\text{var. (error)} + \text{var. (AB)} + \text{var. (B)}}$$

or

$$h^2 = \frac{4\sigma_B^2}{\sigma_{\text{error}}^2 + \sigma_{AB}^2 + \sigma_B^2}$$

PLANTATION NAME	NUMBER OF BLOCKS	% OF TOTAL NUMBER OF FAMILIES PLANTED	h^2
Rye Creek	2	92	.4903
Wolf Creek	4	91	.3143
Condon	2	91	.6830
Lubrecht	3	90	.4585
Meadow Creek	5	91	.5601
Tensed	5	91	.5374
Lone Mountain	5	92	.5491
<hr/>			
Rye Creek	5	57	.3064
Wolf Creek	5	78	.3902
Condon	5	44	.5352
Lubrecht	5	81	.4378

¹ Calculations followed Wright (1921), Falconer (1960) and Namkoong (1979).

representation estimates ranged from .3064 to .5601 according to location. Heritability estimates using 90% or more of the families planted for this study ranged from .3134 to .6830 depending on location. Previous estimates using open-pollinated progeny data for ponderosa pine height growth range from .362 (Squillace and Silen 1962) and .392 (Callaham and Hasel 1961) to .625 (Madsen and Blake 1977). Family heritability estimates on eleven year height ranged from .37 to .53 (Rehfeldt 1980b). Thus, estimates for this study fall well within the range of other published reports of heritability in ponderosa pine. Results clearly indicate substantial genetic variation and that ponderosa pine will respond favorably to selection.

Genetic variation patterns can be clinal (continuous) or ecotypic (discontinuous). One method for interpreting genetic variation patterns uses regression analysis. This unique statistical method was used in an effort to generalize genetic variation patterns. Simple linear regressions on mean seven year total height by family were performed using the elevation, latitude and longitude of seed sources, and simple linear correlation coefficients were computed from a "canned regression" program (Zuuring 1981). These correlation coefficients were statistically nonsignificant for all seven test plantations (Table 7). This implies that seven year total height cannot be accurately predicted through the use of a simple linear relation of seed source elevation, or seed source latitude or seed source longitude.

Caution must be exercised in using regression analyses since the degree or type of association between variables does not necessarily

Table 7. Correlation coefficients for family mean total heights at seven years at each of seven plantations.

	Rye Creek	Wolf Creek	Condon	Lubrecht	Meadow Creek	Tensed	Lone Mountain
Seed Source Elevation	-.275	.294	.060	.146	-.289	-.018	-.085
Seed Source Latitude	.329	-.168	-.065	-.133	.232	.048	.108
Seed Source Longitude	.045	-.224	-.138	-.227	-.078	-.058	-.023

* Statistically significant at $\alpha = 0.01$.

** Statistically significant at $\alpha = 0.05$.

imply a causal relationship. However, causality must be considered. The variation described can be clinal, ecotypic or random. If variation in characters linearly follows environmental gradients, the relationship is clinal. The relationship is considered ecotypic if the variation in characters relates to changes in the environment but does not follow linear gradients. Variation is random if it varies indiscriminantly with respect to changes in the environment.

Often, plotting the data may demonstrate relationships better than a statistical index. Three scattergrams were plotted for each plantation. Family mean total height at seven years was plotted by seed source factors: 1) elevation; 2) latitude; and 3) longitude. No relationships were apparent at any of the plantations for any of the factors. Families spanned the range of heights as well as the elevations, latitudes and longitudes of the seed sources. Since results from the seven plantations were essentially the same, one representative plantation for each factor was chosen for inclusion here (Figures 3, 4 and 5).

The use of juvenile height measurements has shortcomings. However, several high juvenile-parent correlations have been reported in ponderosa pine height growth. Results of a New Zealand ponderosa pine study found strong correlation between height growth of families at ages one and twenty-five years (Moore 1944). Squillace and Silen (1962) found strong correlations between average height per family at two years and average family height at thirty years. In his study, Conkle (1973), found juvenile-mature height correlations were generally strong at low and mid elevation test sites. Results up to twenty years, at the high

Figure 3. Relationship Between Family Mean Seven Year Total Height and Elevation of the Seed Source.

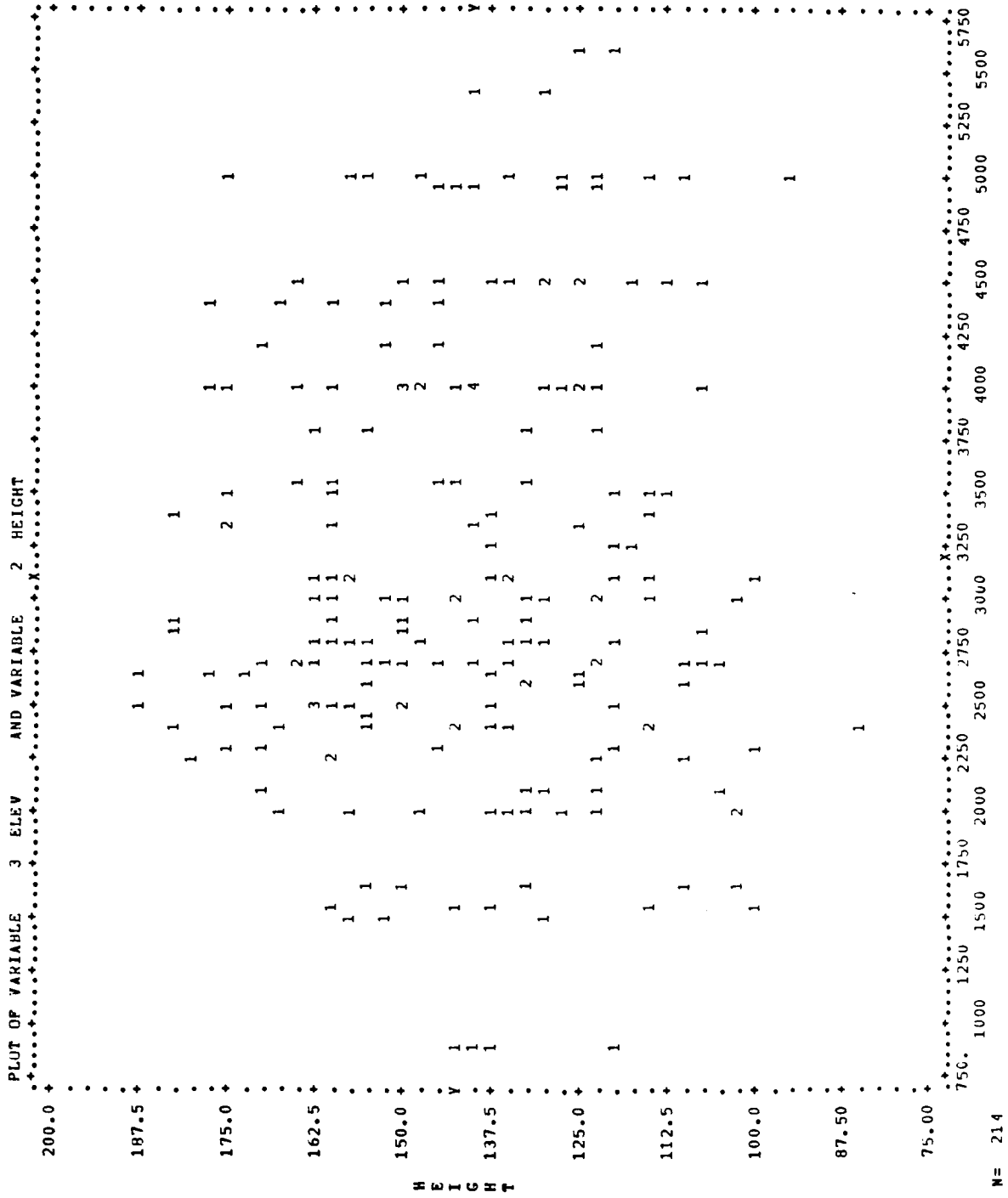


Figure 4. Relationship Between Family Mean Seven Year Total Height and Latitude of the Seed Source.

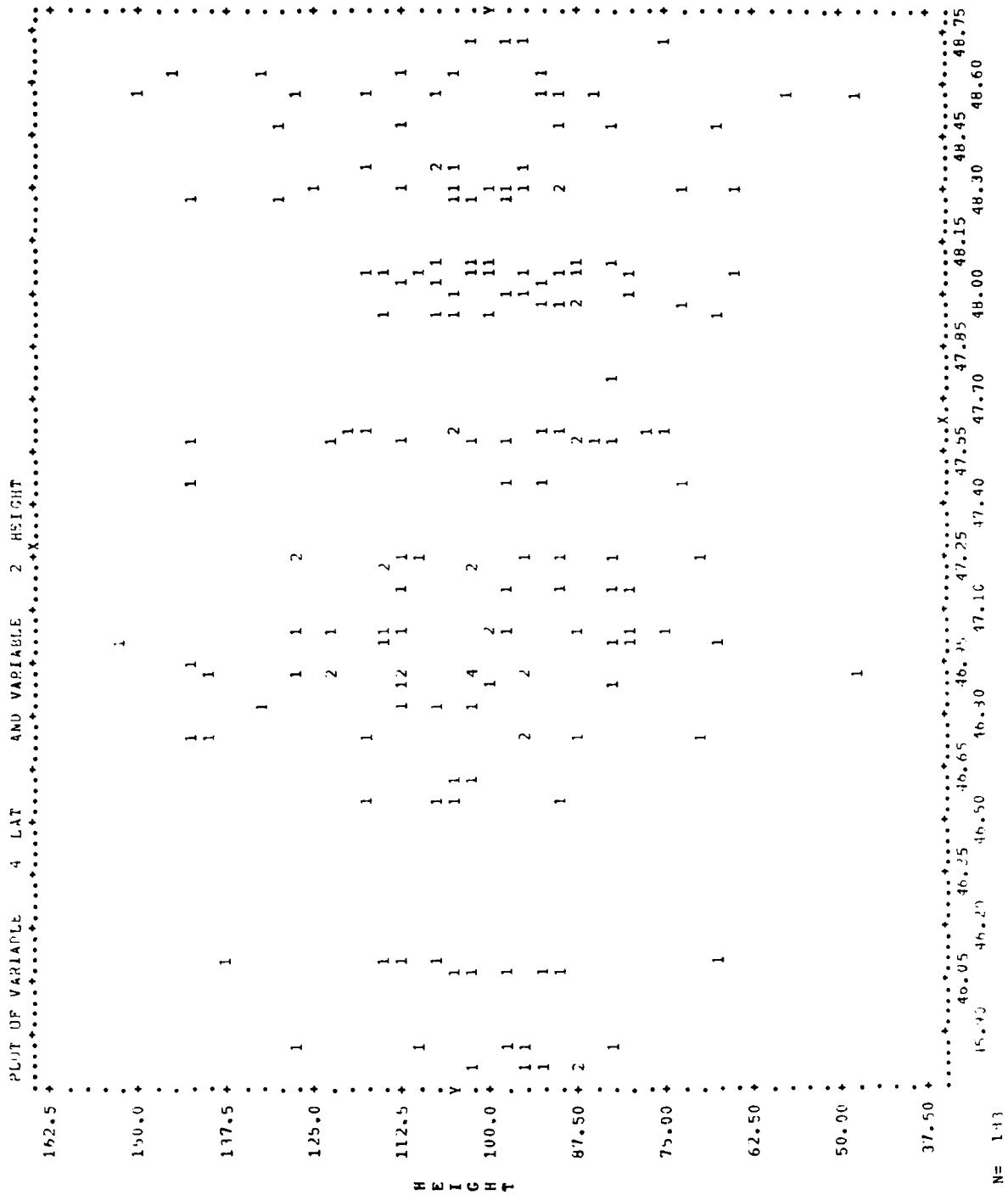
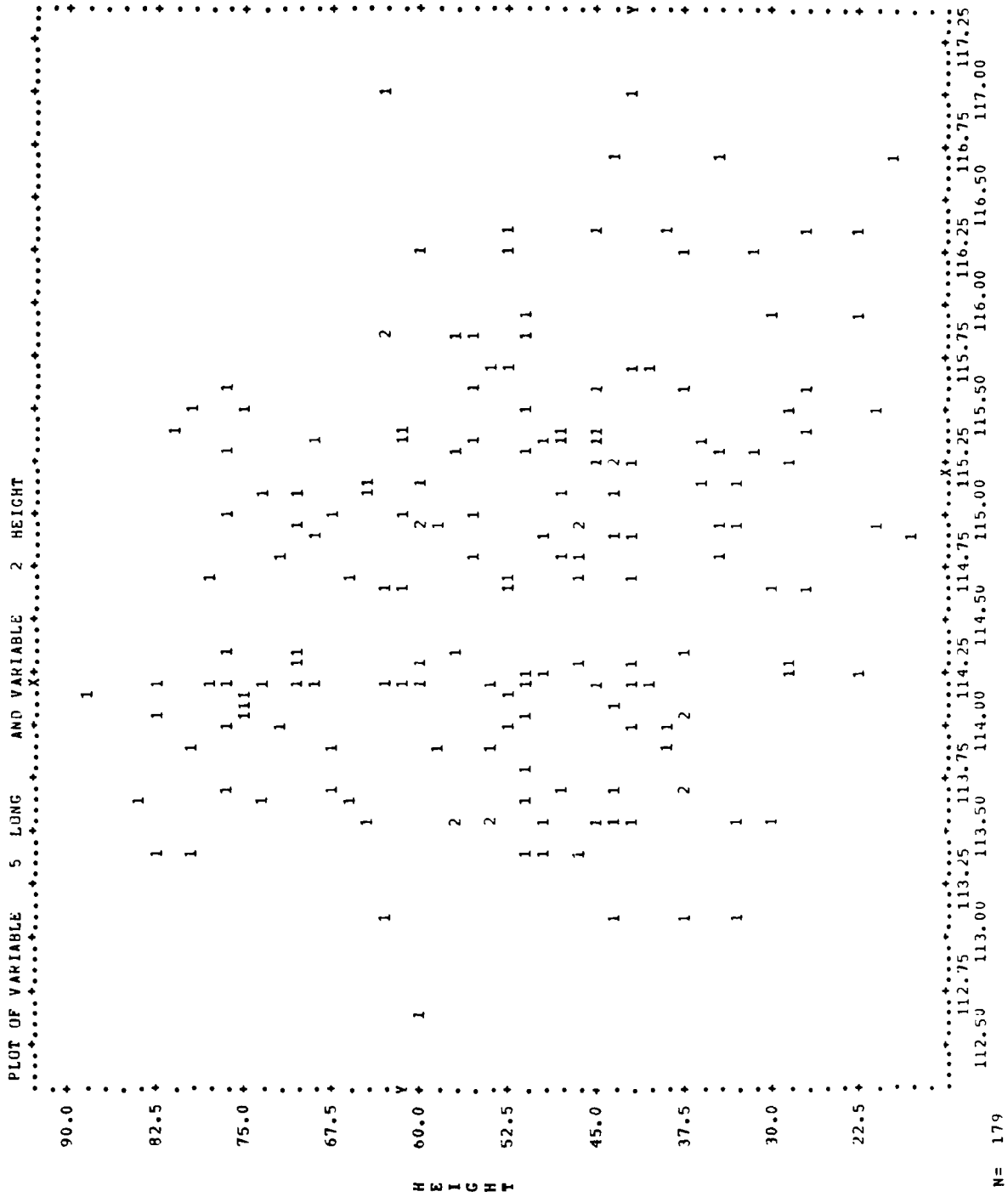


Figure 5. Relationship Between Family Mean Seven Year Total Height and Longitude of the Seed Source.



elevation test site, showed that many of the low and mid elevation progenies grew better. This trend has now changed. The high elevation seed source trees have now outgrown the lower elevation seed source trees at the high elevation site. Steinhoff (1970) reported similar findings. From nineteen sources, the tallest source at age twelve was also the tallest at age fifty, and the shortest at age twelve was also the shortest at age fifty. However, sources ranked 3, 4, and 8 at age twelve dropped to ranks 11, 12, and 16 respectively at age fifty. Conversely, sources ranked 9, 13, and 17 at age twelve now rank 2, 6, and 8 respectively at age fifty.

Statistical analyses of early progeny height data such as the ones in this study can only point out the minimum specifications to be used in establishing seed zone rules. If the elevational variation observed can be largely explained by latitude, then elevation should be of secondary importance for seed zoning in a given geographic subdivision. All environmental factors should be used to establish seed zones for ponderosa pine. The identification of selection pressures and their strengths can serve as a guide toward delineating seed zone boundaries. Selection along geographic gradients nearly always involves the same environmental factor influencing several characters and groups of genes. Thus, variation of an entire character complex may be found along environmental gradients.

Seed zones must be based on numerous adaptational and genetic features. Delineations of seed zones on the basis of multicharacter analyses are less subject to the pitfalls of seed source X environment

interactions than single character analyses. Although state lines are political boundaries that cannot be responsible for genetic differentiation, the boundary between Idaho and Montana roughly follows the crests of the Cabinet and Bitterroot Mountains. These mountains may sufficiently alter westerly air masses to produce macroclimatic provenances that control differentiation. This project of the Inland Empire Tree Improvement Cooperative involves eight test plantations which provide good indications of how far seed can be transferred without loss in total height growth. The results reported represent early performance of provenances for which seed was maintained separately by maternal parent. All trees of a species are not identical. Each tree provides a genetically different yardstick for measuring the environmental factors of a site. Furthermore, the results presented here illustrate the need for caution in calling any planting site "uniform".

SUMMARY AND CONCLUSIONS

The testing of geographic seed sources (provenances) provides one alternative for obtaining genetically superior seed. In this testing program, plantations were established over a range of environmental sites. The observed differential responses of provenances to the range of sites result from genotype X environment interactions. This interaction can be manifested in two ways: 1) by differences in family rank at the various locations; and 2) by differences in relative superiority at the locations when family ranks are the same. The first form requires the selection of provenances for specific environments, while the second allows the selection of a superior provenance for general use. The contribution of an individual provenance to the interaction depends on its phenotypic stability relative to the phenotypic stability of the mean of all provenances. Those with average stability contribute least to the interaction, while provenances that are either more or less stable than the average contribute most.

The objective of this study was to examine genetic variation in seven year total height and describe genetic variation patterns of ponderosa pine in the Inland Empire.

The sample consisted of 434 open-pollinated families plus one bulk stand collection from each of 93 wild stands. The families were planted at seven test plantations located throughout the range of ponderosa pine in the northern Rocky Mountains. Seven year old total height data were obtained from all families at each of the test plantations. Base line diameter measurements and damage index codes were also recorded.

Analysis of variance for each plantation and subsequent F-values showed that families, blocks and the block X family interaction have significant ($\alpha = 0.01$) effects on seven year total height. Family variation within each test plantation appears much greater than the variation due to block or the block X family interaction. It is possible that a substantial proportion of the within family variation results from gene flow from outside the collection area. Narrow-sense heritability estimates at each plantation ranged from .3064 to .6830 depending on the site and number of blocks used. These estimates apply only to the seven year total height. The results clearly indicate substantial genetic variation and that ponderosa pine will respond favorably to selection.

Multiple comparison procedures applied to family mean total height at seven years provided a ranking of families at each plantation from tallest to shortest. Significant differences were evidenced between families at each plantation. Different family rankings and different contrasts were observed between plantations.

Results from simple linear regression analyses support other findings of this study. Correlation coefficients computed showed no significant relationship between family mean seven year total height and the elevation or latitude or longitude of the seed source. Scattergrams plotted by plantation further evidenced nonsignificant relationships. In addition, individual seven year total height could not be predicted from these seed source factors.

This study provides conclusive evidence that specific families perform better at specific sites. Prevalent genotype X environment interactions occurred at all of the test plantations. The results indicate that environmental factors at the seed source need not be a major consideration when selecting seed for planting. However, time may show more distinct differences as evidenced by Steinhoff (1970).

Previous results (Steinhoff 1970 and Conkle 1973) indicate that early performance does not necessarily predict long-term growth. If trees (families) that will continue to be outstanding growers can be recognized from juvenile characteristics, substantial time can be saved in tree improvement. However, until dependable juvenile-mature height growth correlations can be established, the results of this study should be regarded as preliminary and used with caution.

Species that have developed contrasting adaptive genetic systems are products of evolutionary history. Consequently, studies of the ecological genetics of species in the northern Rocky Mountains should continue (Rehfeldt 1979b).

Results from several short-range tests must be known and more time must pass to observe any changes that might occur before the delineation of seed planting zones becomes finalized. Until additional analyses can be made and more results obtained, the use of local seed sources should be enforced for planting ponderosa pine in the northern Rocky Mountains.

REFERENCES CITED

- Adams, W. T., J. H. Roberts, and B. J. Zobel. 1973. Intergenotypic Interactions Among Families of Loblolly Pine (*Pinus taeda* L.). Theoretical and Applied Genetics 43:319-322.
- Allard, R. W. 1965. Genetic Systems Associated with Colonizing Ability in Predominantly Self-pollinated Species. Pages 49-75. In: The Genetics of Colonizing Species, H. G. Baker and G. L. Stebbins, editors. Academic Press, New York, New York.
- Antonovics, J. 1968. Evolution in Closely Adjacent Plant Populations. V. Evolution of Self-fertility. Heredity 23:507-524.
- Austin, L. 1932. Hereditary Variations in Ponderosa Pine. Madrono 2:62-63
- Axelton, E. A. 1974. Ponderosa Pine Bibliography. II. 1966-1970. USDA Forest Service Technical Report INT-12. Intermountain Forest and Range Experiment Station.
- Baldwin, H. I. 1956. The Period of Height Growth in Different Provenances of European Larch. FAO Document 56/2556.
- Bancroft, T. A. 1968. Topics in Intermediate Statistical Methods Volume I. The Iowa State University Press, Ames, Iowa.
- Barber, H. N. 1959. The Process of Natural Selection. Proceedings from the X. International Congress of Genetics, II.
- Barber, J. C. 1964. Inherent Variation Among Slash Pine Progenies at Ida Cason Callaway Foundation. USDA Forest Service Research Paper SE-10. Southeastern Forest Experiment Station.
- Barnes, B. V. 1967. Phenotypic Variation Associated with Elevation in Western White Pine. Forest Science 13:357-364.
- Bey, C. F. 1979. Geographic Variation in *Juglans nigra* in the Midwestern United States. Silvae Genetica 28:132-135.
- Bjorkman, O. and P. Holmgran. 1963. Adaptability of the Photosynthetic Apparatus to Light Intensity in Ecotypes from Exposed and Shaded Habitats. Physiologica Plantarum 16:889-914.
- Bradshaw, A. D. and R. W. Snaydon. 1959. Population Differentiation within Plant Species in Response to Soil Factors. Nature 183:129-130.

- Britton, R. J. and E. H. Davidson. 1969. Gene Regulation for Higher Cells: A Theory. *Science* 165:349-357.
- Brown, A. H. D. 1978. Isozymes, Plant Population Genetics Structure and Genetic Conservation. *Theoretical and Applied Genetics* 52:145-157.
- Burdon, R. D. and J. A. Zabkiewicz. 1973. Identical and Nonidentical Seedling Twins in *Pinus radiata*. *Canadian Journal of Botany* 51:2001-2004.
- Callahan, R. Z. and W. Metcalf. 1959. Altitudinal Races of Ponderosa Pine - Confirmed. *Journal of Forestry* 57:500-502.
- _____ and A. A. Hasel. 1961. *Pinus ponderosa* Height Growth of Wind-pollinated Progenies. *Silvae Genetica* 10:33-42.
- _____ and A. R. Liddicoet. 1961. Altitudinal Variation at 20 Years in Ponderosa and Jeffrey Pines. *Journal of Forestry* 59:814-820.
- Campbell, R. K. 1974. A Provenance-Transfer Model for Boreal Regions Meddr. Norske Skogfors. *Ves.* 31:544-566. Cited by Campbell and Sorensen (1978) in Effects of Test Environment on Expression of Clines and on Delimitation of Seed Zones in Douglas Fir. *Theoretical and Applied Genetics* 51:233-246.
- _____ and A. I. Sugano. 1975. Phenology of Bud-Burst in Douglas Fir Related to Provenance, Photoperiod, Chilling and Flushing Temperature. *Botanical Gazette* 136:290-298.
- _____ and F. C. Sorensen. 1978. Effect of Test Environment on Expression of Clines and on Delimitation of Seed Zones in Douglas Fir. *Theoretical and Applied Genetics* 51:233-246.
- _____. 1979. Genecology of Douglas Fir in a Watershed in the Oregon Cascades. *Ecology* 60(5):1036-1050.
- _____ and J. F. Franklin. 1980. Seed Zone Classification by Habitat Type and Elevation -- A Comparison in Western Oregon. *Forest Science* (in press).
- Clausen, J. D., D. D. Kneek, and W. M. Hiesey. 1940. Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants. Carnegie Institute. Washington Publication No. 520.

- Cockerham, C. C. 1963. Estimation of Genetic Variances. In: Statistical Genetics and Plant Breeding. A Symposium and Workshop sponsored by the Committee on Plant Breeding and Genetics of the Agricultural Board at North Carolina State College. (Hanson, W. D. and R. F. Robinson, eds.) National Academy of Science - National Research Council, Washington, D. C. Publication 982.
- Comstock, R. E. and R. H. Moll. 1963. Genotype X Environment Interactions. In: Statistical Genetics and Plant Breeding. A Symposium and Workshop sponsored by the Committee on Plant Breeding and Genetics of the Agricultural Board at North Carolina State College. (Hanson, W. D. and R. F. Robinson, eds.) National Academy of Science - National Research Council, Washington, D. C. Publication 982.
- Conkle, M. T. 1973. Growth Data for 29 Years from the California Elevational Transect Study of Ponderosa Pine. Forest Science 19:31-39.
- Critchfield, W. B. 1957. Geographic Variation in *Pinus contorta*. Maria Moors Cabot Foundation, Harvard University, Publication No. 3.
- _____ and E. L. Little, Jr. 1966. Geographic Distribution of the Pines of the World. USDA Miscellaneous Publication No. 991.
- Damman, A. W. H. 1964. Some Forest Types of Central Newfoundland and Their Relation to Environmental Factors. Forest Science Monograph No. 8.
- Darlington, C. D. 1958. Evolution of Genetic Systems, 2nd Ed. Oliver and Boyd, Edinburgh. Great Britain. 265 p.
- David, H. A. 1951. Further Applications of Range to the Analysis of Variance. Biometrika 38:393-407.
- Daubenmire, R. and J. B. Daubenmire. 1968. Forest Vegetation of Eastern Washington and Northern Idaho. Washington Agricultural Experiment Station Technical Bulletin No. 60.
- _____. 1978. Plant Geography. With Special Reference to North America. Academic Press, New York, New York.
- Deneke, F. J. and R. A. Read. 1975. Early Survival and Growth of Ponderosa Pine Provenances in East-central Kansas. USDA Forest Service Research Note RM-297. Rocky Mountain Forest and Range Experiment Station.

- Dickman, D. I. and T. T. Kozlowski. 1971. Cone Size and Seed Yield in Red Pine (*Pinus resinosa* Ait.) American Midland Naturalist 85:431-436.
- Dobzhansky, T. 1955. A Review of Some Fundamental Concepts and Problems of Population Genetics. Cold Spring Harbor Symposium Quantitative Biology 20:1-15.
- Donovan, G. A., E. M. Long, J. P. Buijtenen, J. F. Robinson, and R. A. Woessner. 1976. Introduction to Practical Forest Tree Improvement. Texas Forest Service, a part of Texas A and M University System. Circular 207.
- Duffield, J. W. 1963. Integrating Progeny Testing with Forest Production. Northwest Science 37(4):119-125.
- Duncan, D. B. 1955. Multiple Range and Multiple F-Tests. Biometrics 11:1-42.
- Ehrlich, P. R. and P. H. Raven. 1969. Differentiation of Populations. Science 165:1228-1232.
- Endler, J. A. 1973. Gene Flow and Population Differentiation. Science 179:243-250.
- Eneroth, O. 1926. Studies over Risken Vid Avandande Av Tallfio Av Frammande Proveniens, Skogsforsoksanst 23:1-62. Cited by Campbell and Sorensen (1978) in Effect of Test Environment on Expression of Clines and on Delimitation of Seed Zones in Douglas Fir. Theoretical and Applied Genetics 51:233-246.
- Falconer, D. S. 1960. Introduction to Quantitative Genetics. Ronald Press, New York, New York.
- _____. 1975. Introduction to Quantitative Genetics. Longman, London.
- Feret, P. P. 1971. Isozyme Variation in *Picea glauca* (Moench) Voss Seedlings. Silvae Genetica 20:46-50.
- _____. 1974. Genetic Differences Among Three Small Stands of *Pinus pungens*. Theoretical and Applied Genetics 44:173-178.
- Forward, D. F. and N. J. Nolan. 1964. Growth and Morphogenesis in the Canadian Forest Species VII. Progress and Control of Longitudinal Growth of Branches on *Pinus resinosa* Ait. Canadian Journal of Botany 42:923-950.

- Forrest, W. G. and J. D. Ovington. 1971. Variation in Dryweight and Mineral Nutrient Content of *Pinus radiata* Progeny. *Silvae Genetica* 20:174-179.
- Fowler, D. P. 1965. Effects of Inbreeding in Red Pine (*Pinus resinosa* Ait.) II. Pollination Studies. *Silvae Genetica* 14:12-23.
- _____ and R. W. Morris. 1977. Genetic Diversity in Red Pine: Evidence for Low Genic Heterozygosity. *Canadian Journal of Forest Research* 7:343-347.
- Fowells, H. A. 1953. The Effect of Seed and Stock Sizes on Survival and Early Growth of Ponderosa Pine and Jeffrey Pine. *Journal of Forestry* 51:504-507.
- Fryer, J. H. and F. T. Ledig. 1972. Microevolution of the Photosynthetic Temperature Optimum in Relation to the Elevational Complex Gradient. *Canadian Journal of Botany* 50:1231-1235.
- Gashwiler, J. 1967. Conifer Seed Survival in a Western Oregon Clearcut. *Ecology* 48:431-438.
- Gerhold, H. D. 1959. Seasonal Variation of Chloroplast Pigments and Nutrient Elements in the Needles of Geographic Areas of Scotch Pine. *Silvae Genetica* 8:113-123.
- Grossman, M. 1970. Sampling Variance of the Correlation Coefficients Estimated from Analysis of Variance and Covariance. *Theoretical and Applied Genetics* 40:357-359.
- Guries, R. P. and F. T. Ledig. 1978. Inheritance of Some Polymorphic Isozymes in Pitch Pine (*Pinus rigida* Mill.) *Heredity* 40:27-32.
- Habeck, J. R. 1958. White Cedar Ecotypes in Wisconsin. *Ecology* 39:457-463.
- Halloran, G. M. 1975. Genetic Analysis of Plant Height in Wheat. *Theoretical and Applied Genetics* 45:368-375.
- Hamrick, J. and W. J. Libby. 1972. Variation and Selection in Western U. S. Montane Species. I. White Fir. *Silvae Genetica* 21:29-35.
- _____. 1976. Variation and Selection in Western Montane Species. II. Variation Within and Between Populations of White Fir on an Elevational Transect. *Theoretical and Applied Genetics* 47:27-34.
- Hanover, J. W. 1963. Geographic Variation in Ponderosa Pine Leader Growth. *Forest Science* 9:86-95.

- _____ and B. V. Barnes. 1969. Heritability of Height Growth in Western White Pine Seedlings. *Silvae Genetica* 18:80-82.
- Hanson, W. D. 1963. Heritability. In: Statistical Genetics and Plant Breeding. A Symposium and Workshop sponsored by the Committee on Plant Breeding and Genetics of the Agricultural Board at North Carolina State College. (Hanson, W. D. and R. F. Robinson, eds.) National Academy of Science - National Research Council, Washington, D. C. Publication 982.
- Harper, J. L. 1967. A Darwinian Approach to Plant Ecology. *Journal of Applied Ecology* 4:267-290.
- Hartley, H. O. 1946. Studentization or the Elimination of the Standard Deviation of the Parent Population from the Random Sample - Distribution of Statistics. *Biometrika* 33:173-180.
- _____. 1950. The Use of Range In Analysis of Variance. *Biometrika* 37:271-280.
- Hellmers, H. and D. A. Rook. 1973. Air Temperature and Growth of Radiata Pine Seedlings. *New Zealand Journal of Forest Science* 3:271-285.
- Hermann, R. K. and D. P. Lavender. 1968. Early Growth of Douglas Fir from Various Altitudes and Aspects in Southern Oregon. *Silvae Genetica* 17:143-151.
- Heslop-Harrison, J. 1964. Forty Years of Genecology. In: *Advances in Ecological Research* (Cragg, J. D., ed.), Volume 2:159-247, Academic Press, London.
- Holzer, K. 1969. A Late Frost Injury in an Alpine Norway Spruce (*Picea abies* (L) Karst) Provenance Test. Publication 69-6/10, Second World Consultation on Forest Tree Breeding, Food and Agricultural Organization of the United Nations, International Union of Forest Research Organizations, Rome, Italy.
- Huxley, J. S. 1939. Clines: An Auxiliary Method in Taxonomy. *Bijdr. tot. de Dierk.* 27:491-520. Cited by Heslop-Harrison (1964) in *Forty Years of Genecology. Advances in Ecological Research* Volume 2:159-247.
- Irgens-Moller, H. 1957. Ecotypic Response to Temperature and Photoperiod in Douglas Fir. *Forest Science* 3:79-83.
- _____. 1962. Genotypic Variation in Photoperiodic Responses of Douglas Fir Seedlings. *Forest Science* 8:360-362.

- _____. 1967. Patterns of Height Growth Initiation and Cessation in Douglas Fir. *Silvae Genetica* 16:56-58.
- Jackson, M. T. and J. E. Newman. 1967. Indices for Expressing Differences in Local Climates Due to Forest Cover and Topographical Differences. *Forest Science* 13:60-71.
- Jeffers, R. M. and R. A. Jensen. 1980. Twenty-year Results of the Lake States Jack Pine Seed Source Study. USDA Forest Service Research Paper NC-181. North Central Forest Experiment Station.
- Jenkinson, J. L. 1974. Ponderosa Pine Progenies: Differential Response to Ultramafic and Granitic Soils. USDA Forest Service Research Paper PSW-101. Pacific Southwest Forest and Range Experiment Station.
- Jensen, K. F. and G. E. Getherum. 1967. Height Growth of Scotch Pine Seedlings in Relation to Pre-chilling Photoperiod and Provenance. *Iowa State Journal of Science* 41:425-432.
- Keegan, C. E. 1976. Financial Analysis of Alternative Ponderosa Pine Tree Breeding Programs. M. S. Thesis. University of Montana, School of Forestry.
- Khalil, M. A. K. and A. W. Douglas. 1979. Correlation of Height Growth in Black Spruce With Site Factors of the Provenances. *Silvae Genetica* 28:122-124.
- King, J. P. 1965. Seed Source X Environment Interactions in Scotch Pine. *Silvae Genetica* 14:141-148.
- _____. 1966. Ten-year Height Growth Variation in Lake States Jack Pine. USDA Forest Service Research Paper NC-6 North Central Experiment Station.
- Knight, R. 1970. The Measurement and Interpretation of Genotype X Environment Interactions. *Euphytica* 19:225-235.
- Korstain, C. F. 1924. A Silvical Comparison of the Pacific Coast and Rocky Mountain Forms of Western Yellow Pine. *American Journal of Botany* 11:318-324.
- Kramer, P. J. and T. T. Kozlowski. 1960. *Physiology of Trees*. McGraw-Hill Book Company, New York, New York.
- Kung, F. H. and J. W. Wright. 1972. Parallel and Divergent Evolution in Rocky Mountain Trees. *Silvae Genetica* 21:77-85.

- Langlet, O. 1934. Om Variation hos Tullen Pinus Sylvestris Och Dess Samband Med Klimatet. Meddel. Skogsforsoksanst. Stockholm. 27:87-93. Cited by Madsen (1975) in Genecology of *Pinus ponderosa* (Laws.) in the Northern Rocky Mountains. M. S. Thesis, University of Montana, School of Forestry.
- _____. 1936. Studier Over Tallens Fysiologiska Variabilitat Och Dess Samband Med Klimatet. Ett Bilrag Til Kannedommen Om Tallens Ecotyper. Meddel. Fran Statens - Skogsforst Kaanst 29:219-470. Cited by Madsen (1975) in Genecology of *Pinus ponderosa* (Laws.) in the Northern Rocky Mountains. M. S. Thesis, University of Montana, School of Forestry.
- _____. 1945. Om Mojligheterna Att Skogsodla Med Gran-och Tallfio av Ortsframmande Proveniensen. Svenska Skogsvordsfor. Tidskor. 43. Cited by Campbell and Sorensen (1974) in Effect of Test Environment on Expression of Clines and on Delimitation of Seed Zones in Douglas Fir. Theoretical and Applied Genetics 51:233-246.
- _____. 1962. Ecological Variability and Taxonomy of Forest Trees. In: Tree Growth, ed. T. T. Kozlowski. Section 23:357-369.
- _____. 1971. Two Hundred Years of Genecology. Taxon 20(5/6): 653-722.
- Larson, M. M. 1966. Racial Variation in Ponderosa Pine at Fort Valley, Arizona. USDA Forest Service Research Note RM-73. Rocky Mountain Forest and Range Experiment Station.
- Lavender, D. P. and W. S. Overton. 1972. Thermoperiod and Soil Temperatures as They Affect Growth and Dormancy of Douglas Fir Seedlings of Different Geographic Origin. Oregon State University Forest Research Lab Research Paper No. 13.
- _____, G. B. Sweet, J. B. Zaerr, and R. K. Hermann. 1973. Spring Shoot Growth in Douglas Fir May be Initiated by Gibberellins Exported from the Roots. Science 182:838-839.
- Lerner, I. M. 1958. The Genetic Basis of Selection. University of California, Berkeley. John Wiley and Sons, Inc., New York.
- Lester, D. T. 1970. Variation in Seedling Development in Balsam Fir Associated with Seed Origin. Canadian Journal of Botany 48:1093-97.
- _____, R. M. Jeffers, and J. W. Wright. 1976. Provenance and Family Variation in Balsam Fir from Michigan and Wisconsin. Reprinted from Proceedings of the Twelfth Lake States Forest Tree Improvement Conference. USDA Forest Service, General Technical Report NC-26.

Levins, R. 1963. Theory of Fitness in a Heterogeneous Environment. II. Development Flexibility and Niche Selection. *American Naturalist* 97:75-90.

_____. 1964. Theory of Fitness in a Heterogeneous Environment. III. The Response to Selection. *Journal of Theoretical Biology* 7:224-240.

_____. 1965. Theory of Fitness in a Heterogeneous Environment. V. Optimal Genetic Systems. *Genetics* 52:891-904.

_____. 1969. Dormancy as an Adaptive Strategy. *Symposia of the Society for Experimental Biology*. Academic Press, New York.

Libby, W. J., R. F. Stettler, and F. W. Seitz. 1969. Forest Genetics and Forest Tree Breeding. *Annual Review of Genetics* 3:469-494.

_____, W. H. Brener, D. Cole, L. Pugsley, W. I. Stein, and C. E. Furnsworth. 1970. Biological Methods of Securing Genetic Gains in Forest Trees. Reprinted from the Conference on Artificial Regeneration for Multiple Use Forest Management.

_____. 1973. Domestication Strategies for Forest Trees. *Canadian Journal of Forest Research* 3(2):265-276.

Little, E. L., Jr. and W. B. Critchfield. 1965. Subdivisions of the Genus *Pinus* (Pines). USDA Forest Service Miscellaneous Publication No. 1144.

Lotan, J. E. 1967. Cone Serotiny of Lodgepole Pine Near West Yellowstone, Montana. *Forest Science* 13:55-59.

_____. 1968. Cone Serotiny of Lodgepole Pine Near Island Park, Idaho. USDA Forest Service Research Paper INT-52. Intermountain Forest and Range Experiment Station.

Madgwick, H. A. I. 1964. Variations in the Chemical Composition of Red Pine (*Pinus resinosa* Ait.) Leaves: A Comparison of Well Grown and Poorly Grown Trees. *Forestry* 37:87-94.

Madsen, J. L. 1975. Genecology of *Pinus ponderosa* (Laws.) in the Northern Rocky Mountains. M. S. Thesis. University of Montana, School of Forestry.

_____, and G. M. Blake. 1977. Ecological Genetics of Ponderosa Pine in the Northern Rocky Mountains. *Silvae Genetica* 26:1-8.

Mather, K. 1943. Polygenic Inheritance and Natural Selection. *Biological Review* 18:32-64.

- May, J. M. 1952. Extended and Corrected Tables of the Upper Percentage Points of the 'Studentized' Range. *Biometrika* 39:192-193.
- McGee, C. E. 1974. Evolution of Seed Sources and Planting Site Affects Phenology and Development of Red Oak Seedlings. *Forest Science* 20: 160-164.
- McNaughton, S. J. and L. L. Wolf. 1970. Dominance and the Niche in Ecological Systems. *Science* 167:131-139.
- Mettler, L. E. and T. G. Gregg. 1969. Population Genetics and Evolution. Prentiss-Hall Inc., Englewood Cliffs, New Jersey.
- Miksche, J. P. 1976. Modern Methods in Forest Genetics. Proceedings in Life Sciences. Springer-Verlag, New York, New York.
- Mirov, N. T., J. W. Duffield, and A. R. Liddicoet. 1952. Altitudinal Races of Ponderosa Pine -- a 12 Year Progress Report. *Journal of Forestry* 50:825-831.
- _____. 1957. Distribution of Turpentine Components Among Species of the Genus *Pinus*. In: The Physiology of Forest Trees Symposium Proceedings Harvard Forest, K. V. Thiamann (ed.). The Ronald Press Co., New York.
- _____. 1967. The Genus *Pinus*. The Ronald Press Co., New York.
- Moore, A. M. 1944. *Pinus ponderosa* (Douglas) -- Comparison of Various Types Grown Experimentally on Kaingaroa State Forest. *New Zealand Journal of Forestry* 5:42-49.
- Moran, P. A. P. 1951. Partial and Multiple Rank Correlations. *Biometrika* 38:26-32.
- Morgenstern, E. K. 1969a. Genetic Variation in Seedlings of *Picea mariana* (Mill.) BSP. I. Correlation with Ecological Factors. II. Variation Patterns. *Silvae Genetica* 18:151-161.
- _____. 1969b. Genetic Variation in Seedlings of *Picea mariana* (Mill.) BSP. II. Variation Patterns. *Silvae Genetica* 18:161-167.
- _____ and L. Roche. 1969. Using Concepts of Selection to Delimit Seed Zones. Publication 69-2/16, Second World Consultation on Forest Tree Breeding, Food and Agricultural Organization of the United Nations, International Union of Forestry Research Organizations, Rome, Italy.

- _____ and A. H. Teich. 1969. Phenotypic Stability of Height Growth of Jack Pine Provenances. *Canadian Journal of Genetics and Cytology* 11:110-117.
- Namkoong, G. 1966. Inbreeding Effects of Estimation of Additive Genetic Variance. *Forest Science* 12:8-13.
- _____, E. B. Snyder, and R. W. Stonecypher. 1966. Heritability and Gain Concepts for Evaluating Breeding Systems such as Seedling Orchards. *Silvae Genetica* 15:76-84.
- _____ and E. B. Snyder. 1969. Accurate Values for Selection Intensities. *Silvae Genetica* 18:172-173.
- _____. 1979. Introduction to Quantitative Genetics in Forestry. USDA Forest Service Technical Bulletin No. 1588.
- _____ and M. T. Conkle. 1976. Time Trends in Genetic Control of Height Growth in Ponderosa Pine. *Forest Science* 22:2-12.
- Nienstaedt, H. and J. S. Olson. 1961. Effects of Photoperiod and Source on Seedling Growth of Eastern Hemlock. *Forest Science* 7:81-96.
- O'Donald, P. 1967. Genetic Load of an Evolutionary Change. *Nature* 216:1348.
- Odum, E. P. 1969. The Strategy of Ecosystem Development. *Science* 164:262-270.
- Oliver, W. W. and R. F. Powers. 1971. Early Height Growth of Ponderosa Pine Forecasts Dominance in Plantations. USDA Forest Service Research Note PSW-250, Pacific Southwest Forest and Range Experiment Station.
- O'Malley, D. M., F. W. Allendorf, and G. M. Blake. 1979. Inheritance of Isozyme Variation and Heterozygosity in *Pinus ponderosa*. *Biochemical Genetics* 17:233-250.
- Patnaik, P. B. 1950. The Use of Mean Range as an Estimator of Variance in Statistical Tests. *Biometrika* 37:78-87.
- Pearson, E. S. and H. O. Hartley. 1946. Tables of the Probability Integral of the Studentized Range. *Biometrika* 33:89-99.
- _____ and H. O. Hartley. 1966. *Biometrika Tables for Statisticians*. Volume I. 3rd Edition. Cambridge University Press.

- Pearson, G. A. 1950. Management of Ponderosa Pine in the Southwest. USDA Forest Service Agricultural Monograph No. 6.
- Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1974. Forest Habitat Types of Montana. USDA Forest Service General Technical Report INT-34. Intermountain Forest and Range Experiment Station.
- Radwan, M. A. and W. D. Ellis. 1975. Clonal Variation in Monoterpene Hydrocarbons of Vapors of Douglas Fir Foliage. Forest Science 21:63-67.
- Rasmuson, B. and D. Rudin. 1971. Variations in Esterase Zymogram Patterns in Needles of *Pinus sylvestris* from Provenances in Northern Sweden. Silvae Genetica 20:39-41.
- Read, R. A. 1958. The Great Plains Shelterbelt in 1954. Nebraska Agricultural Experiment Station Bulletin No. 441. (Great Plains Agricultural Council Publication No. 16).
- _____. 1980. Genetic Variation in Seedling Progeny of Ponderosa Pine Provenances. Forest Science Monograph No. 23.
- Rehfeldt, G. E. and D. T. Lester. 1966. Variation in Shoot Elongation of *Pinus resinosa* Ait. Canadian Journal of Botany 44:1457-1469.
- _____ and D. T. Lester. 1969. Specialization and Flexibility in Genetic Systems of Forest Trees. Silvae Genetica 18:118-123.
- _____ and R. J. Steinhoff. 1970. Height Growth in Western White Pine Progenies. USDA Forest Service Research Note INT-123 Intermountain Forest and Range Experiment Station.
- _____. 1974a. Genetic Variation of Douglas Fir in the Northern Rocky Mountains. USDA Forest Service Research Note INT-184. Intermountain Forest and Range Experiment Station.
- _____. 1974b. Local Differentiation of Populations of Rocky Mountain Douglas Fir. Canadian Journal of Forest Research 4:399-406.
- _____ and R. G. Cox. 1975. Genetic Variation in a Provenance Test of 16-year-old Ponderosa Pine. USDA Forest Service Research Note INT-201. Intermountain Forest and Range Experiment Station.
- _____. 1977. Growth and Coldhardiness of Intervarietal Hybrids of Douglas Fir. Theoretical and Applied Genetics 50:3-15.
- _____. 1978. Genetic Differentiation in Douglas Fir Populations from the Northern Rocky Mountains. Ecology 59:1264-1270.

- _____. 1979a. Ecotypic Differentiation of Populations of *Pinus monticola* in Northern Idaho -- Myth or Reality? *American Naturalist* 114:627-636.
- _____. 1979b. Adaptive Differentiation of Douglas Fir Populations from the Northern Rocky Mountains. USDA Forest Service General Technical Report INT-64. Intermountain Forest and Range Experiment Station.
- _____. 1979c. Ecological Adaptations in Douglas Fir (*Pseudotsuga menziesii* var. *glauca*) Populations. I. Northern Idaho and Northeast Washington. *Heredity* 43:383-397.
- _____. 1980a. Genetic Gains from Tree Improvement of Ponderosa Pine in Southern Idaho. USDA Forest Service Research Paper INT-263. Intermountain Forest and Range Experiment Station.
- _____. 1980b. Genetic Variation in Southern Idaho Ponderosa Pine Progeny Tests After 11 Years. USDA Forest Service General Technical Report INT-75. Intermountain Forest and Range Experiment Station.
- Robertson, F. W. and E. C. R. Reeve. 1952. Heterozygosity, Environmental Variability, and Heterosis. *Nature* 170:286.
- Roche, L. 1969. A Genecological Study of the Genus *Picea* in British Columbia. *New Phytologist* 68:505-554.
- Rowe, K. E. and K. K. Ching. 1973. Provenance Study of Douglas Fir in the Pacific Northwest Region. II. Field Performance at Age Nine. *Silvae Genetica* 22:115-119.
- Ruby, J. L. 1967. The Correspondence Between Genetic, Morphological and Climatic Variation Patterns in Scotch Pine. I. Variations in Parental Characters. *Silvae Genetica* 16:50-56.
- _____. and J. W. Wright. 1976. A Revised Classification of Geographic Varieties in Scotch Pine. *Silvae Genetica* 25:169-175.
- Sakai, K. I., Y. Miyazaki, and T. Matsuura. 1971. Genetic Studies in Natural Populations of Forest Trees. I. Genetic Variability on Enzymatic Level in Natural Forests of *Thujopsis dolabrata*. *Silvae Genetica* 20:168-173.
- _____. and Y. Miyazaki. 1972. Genetic Studies in Natural Populations of Forest Trees. II. Family Analysis: a New Method for Quantitative Genetic Studies. *Silvae Genetica* 21:149-154.

- _____ and Y. G. Park. 1971. Genetic Studies in Natural Populations of Forest Trees. III. Genetic Differentiation within a Forest of *Cryptomeria japonica*. Theoretical and Applied Genetics 41:13-17.
- Samuel, C. J. A. and R. C. B. Johnstone. 1979. A Study of Population Variation and Inheritance in Sitka Spruce. *Silvae Genetica* 28:26-32.
- Scheffe, H. 1958. The Analysis of Variance. John Wiley and Sons, Inc., New York.
- Schotte, G. 1923. Tallfroets Proveniens - Norrlands Vitigaste Skogsodlingsfroga. Medd. Statens Skogsforsoksanst 20:305-400. Cited by Campbell and Sorensen (1978) in Effect of Test Environment on Expression of Clines on Delimitation of Seed Zones in Douglas Fir. Theoretical and Applied Genetics 51:233-246.
- Simonsen, V. and H. Wellendorf. 1975. Some Polymorphic Isoenzymes in the Seed Endosperm of Sitka Spruce. Forest Tree Improvement 9:5-20.
- Snedecor, G. W. 1956. Statistical Methods. 5th Edition. Iowa State University College Press. Ames, Iowa.
- _____ and W. G. Cochran. 1968. Statistical Methods. Iowa State University Press. Ames, Iowa.
- Sorensen, F. 1967. Two-year Results of a West-East Transect-Provenance Test of Douglas Fir in Oregon. USDA Forest Service Research Note PNW-72. Pacific Northwest Forest and Range Experiment Station.
- _____ and R. K. Campbell. 1971. Correlation between Dates of Floral and Vegetative Flush in Douglas Fir. USDA Forest Service Research Note PNW-143. Pacific Northwest Forest and Range Experiment Station.
- _____. 1973. Frequency of Seedlings from Natural Self-fertilization in Coastal Douglas Fir. *Silvae Genetica* 22:20-24.
- _____ and W. K. Ferrell. 1973. Photosynthesis and Growth of Douglas Fir when Grown in Different Environments. Canadian Journal of Botany 51:1689-1698.
- _____ and R. S. Miles. 1974. Self-pollination Effects on Douglas Fir and Ponderosa Pine Seeds and Seedlings. *Silvae Genetica* 2:135-138.

- _____. 1979. Provenance Variation in *Pseudotsuga menziesii* Seedlings from the var. *menziesii* - var. *glauca* Transition Zone in Oregon. *Silvae Genetica* 28:96-103.
- Squillace, A. E. and R. T. Bingham. 1958. Localized Ecotypic Variation in Western White Pine. *Forest Science* 4:20-34.
- _____. and R. R. Silen. 1962. Racial Variation in Ponderosa Pine. *Forest Science Monograph* No. 2.
- _____. 1966. Geographic Variation in Slash Pine. *Forest Science Monograph* No. 10.
- _____. 1974. Average Genetic Correlations Among Offspring from Open-pollinated Forest Trees. *Silvae Genetica* 23:149-156.
- Stebbins, G. L. 1957. Variation and Evolution in Plants. Columbia University Press, New York.
- Steele, R. G. D. and J. H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill, New York, New York.
- Steinbeck, P. F. 1966. Site, Height and Mineral Nutrient Control Relations of Scotch Pine Provenances. *Silvae Genetica* 15:42-50.
- Steinhoff, R. J. 1970. Northern Idaho Ponderosa Pine Racial Variation Study -- 50 Year Results. USDA Forest Service Research Note INT-118. Intermountain Forest and Range Experiment Station.
- _____. and R. J. Hoff. 1971. Estimates of the Heritability of Height Growth in Western White Pine Based on Parent-Progeny Relationships. *Silvae Genetica* 20:142-143.
- _____. 1979. Variation in Early Growth of Western White Pine in North Idaho. USDA Forest Service Research Paper INT-222. Intermountain Forest and Range Experiment Station.
- Stern, K. and L. Roche. 1974. Genetics of Forest Ecosystems. Springer-Verlag, New York.
- Stonecypher, R. W., B. J. Zobel, and R. Blair. 1973. Inheritance Patterns of Loblolly Pines from a Non-selected Natural Population. North Carolina Agricultural Experiment Station, Technical Bulletin No. 220.
- Tauer, C. G., C. A. Mohn, and W. H. Cromwell. 1974. Early Performance of Ponderosa Pine Seed Sources in Minnesota. University of Minnesota, College of Forestry, Minnesota Forest Research Note No. 252.

- _____ and R. L. Gardner. 1978. Nine-year Performance of a Central Oklahoma Planting of Ponderosa Pine Provenances. Oklahoma Agricultural Experiment Station Bulletin B-737.
- Thoday, J. M. 1953. Components of Fitness. Society for Experimental Biology Symposia 7:96-113.
- _____. 1958. Homeostasis in a Selection Experiment. Heredity 12: 401-415.
- Thompson, C. M. and M. Merrington. 1946. Tables for Testing the Homogeneity of a Set of Estimated Variances. Biometrika 33:296-304.
- Tigerstedt, P. M. A. 1974. The Application of Ecological Principles to Forest Tree Breeding. Silvae Genetica 23:62-67.
- Townsend, A. M., J. W. Hanover, and B. V. Barnes. 1972. Altitudinal Variation in Photosynthesis, Growth, and Monoterpene Composition of Western White Pine (*Pinus monticola* Dougl.) Seedlings. Silvae Genetica 21:133-139.
- _____, J. W. Wright, W. F. Kwolek, W. F. Beineke, D. T. Lester, C. A. Mohn, and A. F. Dodge. 1979. Geographic Variation in Young Red Maple Grown in North Central United States. Silvae Genetica 28:33-36.
- Turesson, G. 1922. The Genotypic Response of the Plant Species to the Habitat. Hereditas 3:211-350.
- _____. 1923. The Scope and Importance of Genecology. Hereditas 4:171-176.
- USDA Forest Service. 1965. Silvics of Forest Trees of the United States. Agricultural Handbook No. 271.
- _____. 1973. The Outlook for Timber in the United States -- A Report of the Findings of the 1970 Timber Review. 376 pp.
- Van Deusen, J. L. 1974. Five-year Results of a Ponderosa Pine Provenance Study in the Black Hills. USDA Forest Service Research Note RM-278. Rocky Mountain Forest and Range Experiment Station.
- _____. 1980. Ponderosa Pine Provenances for the Northern Great Plains. USDA Forest Service Research Paper RM-223. Rocky Mountain Forest and Range Experiment Station.
- Van Valen, L. 1965. Morphological Variation and Width of the Ecological Niche. American Naturalist 99:377-390.

- Waddington, C. H. 1942. Canalization of Development and the Inheritance of Acquired Characters. *Nature* 150:560-565.
- Wakeley, P. C. 1961. Results of the Southwide Pine Seed Source Study Through 1960-61. pp. 10-24. In: Proceedings from the 6th Southern Conference of Forest Tree Improvement, Gainesville, Florida.
- Wallace, B. 1968. Topics in Population Genetics. W. W. Norton and Co., New York.
- Waller, R. A. and D. B. Duncan. 1969. A Bayes Rule for Systematic Multiple Comparison Problems. *Journal of the American Statistical Association* 64:1484-1503.
- Wang, C. W. 1967. The Genetic Improvement of Ponderosa Pine in Idaho. University of Idaho. Forest, Wildlife and Range Experiment Station Note No. 7. Moscow, Idaho.
- _____ and R. K. Patee. 1973. Progeny Performance of 271 Ponderosa Pine Parents. Western Forest Genetics Association Symposium. Coeur d'Alene, Idaho.
- _____ and R. K. Patee. 1974. Variation in Seed Characteristics and Seedling Growth of Open-pollinated Ponderosa Pine Progenies. University of Idaho. Forest, Wildlife and Range Experiment Station Paper 15. Moscow, Idaho.
- _____ and R. K. Patee. 1976. Regional Variation in Ponderosa Pine, the 5-year Result. University of Idaho. Forest, Wildlife and Range Experiment Station Bulletin 10. Moscow, Idaho.
- _____. 1977. Genetics of Ponderosa Pine. USDA Forest Service Research Paper WO-34. Washington, D. C.
- Weidman, R. H. 1939. Evidences of Racial Variation in a 25-year Test of Ponderosa Pine. *Journal of Agricultural Research* 59:855-868.
- Wells, O. O. 1964a. Geographic Variation in Ponderosa Pine. I. The Ecotypes and Their Distribution. *Silvae Genetica* 13:89-103.
- _____. 1964b. Geographic Variation in Ponderosa Pine. II. Correlations Between Progeny Performance and Characteristics of the Native Habitat. *Silvae Genetica* 13:126-164.
- Whitaker, R. H. 1957. Recent Evolution of Ecological Concepts in Relation to the Eastern Forests of North America. *American Journal of Botany* 44:197-206.

- _____. 1965. Dominance and Diversity in Land Plant Communities. *Science* 147:250-260.
- Wiersma, J. H. 1963. A New Method for Dealing with Results of Provenance Tests. *Silvae Genetica* 12:200-215.
- Wright, J. W. 1952. Pollen Dispersion of Some Forest Trees. USDA Forest Service Station Paper No. 46. Northeastern Forest Experiment Station.
- _____. 1962. Genetics of Forest Tree Improvement. Publication 62-4/10. First World Consultation on Forest Tree Breeding, Food and Agricultural Organization of the United Nations, International Union of Forest Research Organizations, Rome, Italy.
- _____. 1963. Genetic Variation Among 140 Half-sib Scotch Pine Families Derived from 9 Stands. *Silvae Genetica* 12:83-89.
- _____ and W. I. Bull. 1963. Geographic Variation in Scotch Pine. *Silvae Genetica* 12:1-25.
- _____, S. S. Pauley, R. B. Polk, J. J. Jokela, and R. A. Read. 1966. Performance of Scotch Pine Varieties in the North Central Region. *Silvae Genetica* 15:101-110.
- _____, W. A. Lemmen, and J. N. Bright. 1969. Early Growth of Ponderosa Pine Ecotypes in Michigan. *Forest Science* 15:121-129.
- _____, F. H. Kung, R. A. Read, W. A. Lemmen, and J. N. Bright. 1971. Genetic Variation in Rocky Mountain Douglas Fir. *Silvae Genetica* 20:54-60.
- _____. 1976. Introduction to Forest Genetics. Academic Press, Inc., New York.
- Wright, S. S. 1921. Correlation and Causation. *Journal of Agricultural Research*. XX(7):557-586.
- _____. 1943. Isolation by Distance. *Genetics* 28:114-138.
- Zobel, D., B. A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of Environment to Composition, Structure, and Diversity of Forest Communities of the Central Western Cascades of Oregon. *Ecological Monographs* 46:135-156.
- Zuuring, H. R. 1980 and 1981. Personal Communication. Research Biometrician, School of Forestry, University of Montana.

APPENDIX A

Members of the Inland Empire Tree Improvement Cooperative

Appendix A: Members of the Inland Empire Tree Improvement Cooperative.

Industry:

Boise Cascade Corporation
Burlington Northern, Inc.
Champion International Corporation
Diamond International Corporation
Inland Empire Paper Company
Port Blakely Mill Company
Potlatch Corporation
St. Regis Paper Company
Washington-Idaho Forest Products

Tribal Councils, Bureau of
Indian Affairs:

Coeur d'Alene Tribe of Idaho
Colville Confederated Tribes
Confederated Salish and
Kootenai Tribes of the
Flathead Indian Reservation
Spokane Tribe of Indians

United States Government:

USDA Forest Service, Region 1
USDA, Intermountain Forest and
Range Experiment Station
USDI, BLM, Idaho State Office
USDA, BLM, Montana State Office

States:

Idaho, Department of Lands
Montana, DNRC Division of Forestry
Washington, Department of Natural
Resources

Universities:

University of Idaho
University of Montana
Washington State University

APPENDIX B

Locations, Number of Families Planted and the
Cooperator Responsible for Each Test Plantation

Appendix B: Location, Number of Families Planted and the Cooperator Responsible for Each Test Plantation.

LOCATION	NUMBER OF FAMILIES PLANTED	COOPERATOR RESPONSIBLE
Rye Creek, Montana	86	Burlington Northern, Inc.
Condon, Montana	204	USFS Region 1
Lubrecht, Montana	203	University of Montana
Little Wolf Creek, Montana	118	St. Regis Paper Company
Lone Mountain, Idaho	237	USFS Region 1
Meadow Creek, Idaho	96	USFS Region 1
Tensed, Idaho	237	Idaho Department of Lands
Elijah, Washington	has been replanted	Colville Confederated Tribes

APPENDIX C

Example of a Field Data Recording Form

Appendix C: Example of a Field Data Recording Form.

LUBRECHT PLANTATION											
P L A N T #	B L O C K	ROW	COL	PROG NUM.	YR P L A N T E	76HT CM	78HT CM	79HT CM	DIA AT 30CM MM	DAM IND	REMARKS
6	5	20	2	522	75C	08					
6	5	20	3	522	75C						
6	5	20	4	522	75C	08					
6	5	20	5	522	75C	13					
6	5	20	6	258	75C	15					
6	5	20	7	258	75C	09					
6	5	20	8	258	75C	13					
6	5	20	9	258	W						
6	5	20	10	257	75C	08					
6	5	20	11	257	W	10					
6	5	20	12	257	75C	09					
6	5	20	13	257	W						
6	5	20	14	260	75C	11					
6	5	20	15	260	75C						
6	5	20	16	260	75C	08					
6	5	20	17	260	75C	09					
6	5	20	18	256	R						
6	5	20	19	256	75C	10					
6	5	20	20	256	R	13					
6	5	20	21	256	75C						
6	5	20	22	259	75C	07					
6	5	20	23	259	B	08					
6	5	20	24	259	B	27					
6	5	20	25	259	B						
6	5	20	26	1451	75C	08					
6	5	20	27	1451	75C	27					
6	5	20	28	1451	75C	10					
6	5	20	29	1451	R	11					

APPENDIX D

Damage Index Codes

Appendix D: Damage Index Codes.

FROST

- 0 = NO DAMAGE
- 1 = LIGHT NEEDLE
- 2 = HEAVY NEEDLE AND/OR BUDS DAMAGED BUT NOT KILLED
- 3 = BUDS KILLED
- 4 = LIGHT STEM KILL (TERMINAL FOR 78 GROWTH)
- 5 = HEAVY STEM KILL (TERMINAL FOR MORE THAN 1 YEAR'S GROWTH)
- 6 = BUDS KILLED BUT HAS ADVENTITIOUS BUDS ON TERMINAL
- 7 = LIGHT STEM KILL (TERMINAL & LATERALS - SAME AS 4)
- 8 = HEAVY STEM KILL (TERMINAL & LATERALS - SAME AS 5)
- 9 = DEAD

SHOOT BORER

- 0 = NO DAMAGE
- 1 = 1 OR MORE LATERALS IN 77, 78, 79
- 2 = 77 TERMINAL & EARLIER
- 3 = 78 TERMINAL
- 4 = 79 TERMINAL
- 5 = MULTIPLE ATTACKS (EXTENSIVE YEAR AFTER YEAR)

Appendix D (continued):

BIG GAME

- 0 = NO DAMAGE
- 1 = NEEDLES BROWSED
- 2 = LATERALS NIPPED OFF
- 3 = 77 TERMINAL NIPPED OFF
- 4 = 78 TERMINAL NIPPED OFF
- 5 = 78 TERMINAL AND LATERALS NIPPED OFF
- 6 = 79 TERMINAL NIPPED OFF
- 7 = 79 TERMINAL AND LATERALS NIPPED OFF
- 8 = REPEATED BROWSE ON TERMINAL (2 OR MORE YEARS)
- 9 = ADVENTITIOUS BUDS ON TERMINAL

DIRECTION OF LATERAL MEASURED

- 1 = NORTH
- 2 = EAST
- 3 = SOUTH
- 4 = WEST

PORCUPINE

- 0 = NO DAMAGE
- 1 = BITE OR OLD WOUND
- 2 = LIGHT DAMAGE

Appendix D (continued):

PORCUPINE (CONT'D.)

3 = MODERATE DAMAGE

4 = HEAVY DAMAGE

5 = DEAD (GIRDLED)

LAMUS

0 = NONE

1 = LATERAL ONLY

2 = TERMINAL ONLY

3 = TERMINAL AND LATERAL

GENERAL

1 = MECHANICAL (INCLUDES COWS TRAMPLING)

2 = COMPETITION FROM OTHER VEGETATION

3 = GNARLED AND/OR BUSHY

4 = RODENT UNKNOWN (MICE-GOPHER-RABBIT)

5 = WESTERN GALL RUST

6 = FORKING (CAUSE UNKNOWN)

7 = CHLOROTIC NEEDLES

8 = NEEDLE CAST

9 = NEEDLE MINER

APPENDIX E

Calculations of the Coefficients for the
Expected Mean Squares and F-Values

Appendix E. Calculations of the Coefficients for the Expected Mean Squares and F-values.

n_B = number of blocks retained

n_F = number of families retained

nv_j = number of seedlings/block within jth family, $j = 1, \dots, n_F$

nu_i = proportion of seedlings between i blocks over all families,
 $i = 1, \dots, n_B$

Now Compute:

$$nu_{.} = \sum_{i=1}^{n_B} nu_i, \quad nv_{.} = \sum_{j=1}^{n_F} nv_j$$

$$nu_{.}' = \sum_{i=1}^{n_B} nu_i^2, \quad nv_{.}' = \sum_{j=1}^{n_F} nv_j^2$$

and

$$u^* = nu_{.}' / (nu_{.})^2$$

$$v^* = nv_{.}' / (nv_{.})^2$$

then:

$$K_1 = K_2^* (v^* - 1/n_F)$$

$$K_3 = K_4^* (u^* - 1/n_B)$$

$$K_2 = (nu_{.}) (nv_{.}) (1 - u^*) / (n_B - 1)$$

$$K_4 = (nu_{.}) (nv_{.}) (1 - v^*) / (n_F - 1)$$

$$K_5 = (nu_{.}) (nv_{.}) (1 - u^*)(1 - v^*) / ((n_B - 1)(n_F - 1))$$

because this study used:

$$nu_i = 1$$

then

$$nu_{\cdot} = nu'_{\cdot} = n_B$$

and

$$u^* = 1/n_B$$

$$\therefore K_3 = 0$$

$$K_2 = nv_{\cdot}$$

$$K_5 = K_2 (1 - v^*) / (n_F - 1)$$

$$K_4 = n_B (K_5)$$